ological Agents
Pest Control

Status and Prospects

U.S. Department of Agriculture

in Cooperation with the Land-Grant Universities
State Departments of Agriculture
and the Agricultural Research Institute

BIOLOGICAL AGENTS FOR PEST CONTROL
Status and Prospects

The Report of a Special
Study Team Coordinated by the
Office of Environmental Quality Activities

U.S. Department of Agriculture
In Cooperation with the
Land-Grant Universities
State Departments of Agriculture
and the
Agricultural Research Institute

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FOREWORD

Modern technology and other developments have enabled man to exert an enormous impact on the environment of our planet and its resources. Modern agriculture, one facet of these developments, has thus far enabled us to avoid calamitous shortages of the essentials for human life in the developed countries. This accomplishment is dependent primarily on fossil fuel as an energy source and has not allayed the possibility of future massive food shortages.

As we look ahead to the needs of future generations, it becomes evident that constant attention must be directed to the efficiency of production processes. High on the list of objectives are maximum use of renewable resources and maintenance of the diversity of life in general that will assure preservation and enhancement of our environment.

The protection of agricultural crops, forest, and man and his domestic animals from annoyance and damage by various kinds of pests remains a chronic problem. As we endeavor to improve production processes and develop more effective and acceptable protection tactics, priority must be given to all potentially useful techniques for the control or management of pests as an integral part of the agricultural production process and for maintaining a desired quality of living.

In his 1977 environmental message to Congress, President Carter instructed the Council on Environmental Quality to recommend actions which would encourage development and application of pest management techniques that emphasize use of natural biological controls. The United States Department of Agriculture recognizes the importance of biological control as an essential part of pest management systems. To insure that proper attention be given to the use of biological agents, the Chairman of the Department's Environmental Quality Committee approved the establishment of a Departmental working group on biological agents for pest control under the authority of Secretary's Memorandum No. 1890 entitled "USDA Program for Environmental Quality." This working group, which is composed of representatives from the Agricultural Research Service, Animal and Plant Health Inspection Service, Cooperative State Research Service, Economic Research Service, Extension Service, Forest Service, and Office of General Counsel, recognized the need for obtaining broad-based inputs from

the agricultural community. The working group sponsored a special study to assess the status and to prepare a technical report on the use of biological agents for pest control. This report is the result of that effort. It highlights a number of opportunities for the expanded use of beneficial arthropods, nematodes, snails, microorganisms, and vertebrates for suppression of many kinds of pests. The Department will consider how to best implement the recommendations of this report to increase activities among all concerned in the research, development, and use of biological agents in the management of pest problems.

M. Rupert Cutler
Assistant Secretary
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SUMMARY AND RECOMMENDATIONS

Pest control is an acceptable and necessary part of modern agriculture and forestry, and is required for the protection of public health and welfare. However, some of the methods used during the past three decades have produced some undesirable side effects. Future needs for pest control can be expected to increase, and, as they do, prevailing conditions and attitudes are likely to dictate an increased emphasis on pest management systems which include the use of alternative methods such as biological control agents.

This report is concerned only with the use of biological agents, including vertebrates, insects, mites, nematodes, and a great variety of microbial organisms and microbial products, for pest control. The pests considered are weeds, plant pathogens, insects and mites that attack plants and animals, and nematodes or other invertebrates and microbial organisms that are pests of plants. Scientific and economic matters pertaining to the use of biological agents for control of these pests are discussed, together with regulatory matters and institutional structures; also discussed is the need for the private sector to accomplish research and to implement desirable programs. Recommendations applicable to the broad field of biological agents for pest control are incorporated in this summary.

The practical feasibility of using biological agents, chiefly insects and mites, for the control of many insect pests and weeds has been amply demonstrated, and the basic principles relevant to the operational aspects of the use of these agents are reasonably well understood. The use of pathogens for the control of insect pests shows promise, provided efficacy and safety of such agents can be demonstrated adequately. The use of antagonists for the control of plant pathogens, feasible on a much broader scale than has thus far been demonstrated, depends to a considerable extent upon appropriate manipulation of environmental factors. Nematodes, as well as some other invertebrates other than insects and mites, show potential as useful biological agents though not as yet exploited in a practical way. Birds, mammals, and some other vertebrates are, under some circumstances, important in pest control although their efficient management and manipulation has not yet been demonstrated to be practical.

The following explanatory comments and recommendations deal with scientific and institutional matters deserving of priority action:

(1) The effectiveness of many types of biological agents for pest control is well known; however, much research and development will be required to establish the efficacy and economic feasibility of others. Even among the kinds known to be effective, the full range of potentially useful species is scarcely known and only partially exploited. In view of the potential of biological agents, an intensive effort to discover and make maximum use of these natural resources is fully justified.

Recommendation. Expand current foreign explorations to insure a worldwide search for biological agents associated with taxonomic groups containing known or potential pest species. Biosystematic studies and evaluation processes necessary to select races and strains of agents having greatest potential for pest control should also be undertaken.

(2) An understanding of the degree of specificity in the agent/host relationship is critical to the effective use of biological control agents. This kind of interrelationship often involves complex physiological and behavioral processes about which only limited information is available. A better understanding of this phenomenon would clearly improve our comprehension of the probable host range of biotic agents and hence their efficacy and safety under different conditions of use.

Recommendation. Mount an intensive coordinated research program to better understand genetical, physiological, nutritional, and behavioral characteristics of microbial biota and invertebrate animals.

(3) Present knowledge of the many complex interactions involved in the use of biological agents for pest control is inadequate to permit *a priori* determination of success or failure of broadly based action programs. Even with the advantage of hindsight gained from reviews of past efforts, we have little evidence that permits useful generalizations concerning the ecology of colonization of biological agents. Most such work has been conducted on an empirical basis with little or no control over environmental factors or other concurrent events that

might profoundly affect the outcome of the undertaking. There is urgent need to develop more objective means of appraising the potential success of biological control undertakings and determining, before major action programs are undertaken, how biological agents may be used either concurrently or sequentially in conjunction with other pest management tactics and with production practices.

Recommendation. Give high priority to field trials designed to evaluate the technical feasibility and economic practicality of various methods of biological control and acquire data useful for developing general principles. Further research on production, storage, formulation, and application techniques is needed to insure an acceptable quantity and quality of biological agents. Trials and programs should be used to evaluate how biological agents can best be integrated into evolving strategies of pest and resource management.

(4) The successful use of biological agents for pest control often depends upon measures that attempt to limit the severity of disruptions in the ecosystem. This is the rationale behind using biological agents that are expected to become permanent members of the ecosystem. Inasmuch as pest control is but one of many resource management actions customarily undertaken, the ecosystem adjustments can best be understood on the basis of interactions between the biotic and abiotic environmental components.

Recommendation. Encourage, by all possible means, the development and the application of fundamental knowledge of population biology and methods of ecosystem analysis and modeling useful in the solution of pest control problems in general, and, in particular, to those problems for which the use of biological agents is contemplated.

(5) The relative merits of certain biological control agents have been well demonstrated on a limited scale, but large-scale implementation has lagged seriously.

Recommendation. Initiate and expand area-wide cooperative State/Federal/private sector implementation programs with biological control agents for which sufficient technological bases have been established.

(6) The use of known biocontrol agents is hampered by the lack of efficient access to accumulated information dealing with alternative methods of pest control. Although computer technology is applicable to this task, there is no comprehensive information system for making the needed information readily available at the operational level.

Recommendation. Establish a national information storage and coordinating system specifically designed for assembling and collating domestic and international information relevant to all biological agents that might be used for pest control.

(7) At present, governmental agencies, educational institutions or research laboratories, and a few commercial concerns are suppliers of biological control agents. The extent to which private enterprise may eventually be able to meet future needs will be determined on the basis of economic assessment of opportunities for profit. Profit incentives during the initial stages of developing and testing biocontrol tactics must be more clearly delineated so that economic considerations are not an impediment to more active participation on the part of private enterprise.

Recommendation. Provide additional technical assistance to potential users of biological control agents and assess the need for various types of incentives to private enterprise to encourage and hasten participation in the development and use of biological agents for pest control. Such assistance should be made available to pest management consultants, grower cooperatives, and commercial production and distribution enterprises.

(8) Acquisition of knowledge about organisms and ecosystems necessary to permit maximum use of biocontrol agents will depend upon participation and commitment of many segments of the scientific community.

Recommendation. Expand the U.S. Department of Agriculture's competitive grants/contracts research program in order to focus expertise on existing or emerging solutions of problems through the use of biological control agents. Such a program would provide support for qualified scientists wherever located, including educational institutions, research foundations, private investigators, commercial enterprises, and Federal and State agencies.

(9) Efficacy and environmental impact, as well as economic and social acceptability, must be included in the appraisal of alternative pest control strategies because use of biological control agents often has long term effects whereas other control methods may have only short term effects. A quantitative comparison is difficult. Adequate methodology for such appraisals is not available.

<u>Recommendation. Increase interdisciplinary efforts involving the several appropriate disciplines of biology, economics, and sociology to develop methodology suitable for evaluating comparative benefits and costs of biological control agents and to evaluate the use of specific biological control agents.</u>

(10) Existing legislation concerning pest control is complex, and that related to the use of biological control agents requires clarification.

<u>Recommendation. Review existing legislation and associated regulations that concern pest control, with the specific objectives of clarifying the scope and intent of such laws as they pertain to biological agents; and, if needed, recommend legislation to encourage and expedite expansion of the use of biological control agents.</u>

(11) Effective coordination and implementation of broadly based programs will necessitate an organizational structure with responsibility for making recommendations on research and operational priorities specifically concerned with the use of biological agents for pest control. Recommendations on research and operational priorities should reflect the collective views of scientists in applied ecology and pest control.

<u>Recommendation. Establish a coordinating group to provide a national focus for research, development, and implementation of programs involving the use of biological control agents. This group should be composed of representatives from Federal and State agencies, the private sector, and the general public.</u>

I. INTRODUCTION

Pest control is recognized as an acceptable and necessary part of modern agriculture and forestry and required for protection of public health and welfare. Methods employed vary greatly and tend to reflect compromises involving the three determining factors: Technological capability, economic feasibility, and social acceptability. However, these factors are also subject to change with time, for each involves value judgments based on available information, cost/benefit considerations, the seriousness of the pest problem, and the political climate. Whatever the method chosen, energy resources continue to dwindle under the impact of burgeoning population, and it is inevitable that greater reliance must be placed upon renewable resources in pest management. One alternative is the use of a pest management method that uses energy of the pest's own biomass to fuel a self-perpetuating control system.

Use of biological agents for pest control has long been an integral part of the pest management strategy in forestry and crop production and in the protection of man and animals. The importance and unique advantages of this method of control are well recognized; numerous treatises deal with its accomplishments and methodologies, and there have been significant developments in it in the past decade. The implementation of new pest management tactics and concomitant changes in production methods will require increased reliance on biological methods. With increased understanding of the genetics and population biology of biocontrol agents and of the factors that influence their behavior, the practical application of these methods becomes more complicated but potentially more useful. In addition, the use of biological agents for regulation of pests is inextricably interconnected with socio-economic and environmental factors that cannot be ignored.

This report is concerned with the use of biological agents for the regulation of pest populations. It deals with biological agents useful for the control of weeds, plant pathogens, nematodes, insects and mites attacking plants, as well as microorganisms and other invertebrates that are pests of animals and man. The scope of the report does not include a discussion of resistant varieties, chemical pesticides, cultural practices, environmental modifications, the use of lures and repellants, and

similar practices except as such factors may affect the well-being of biological agents and enhance their effectiveness.

Although living organisms used for pest control are sometimes considered to be "pesticides," under the definition of pesticide in the Federal Insecticide, Fungicide, and Rodenticide Act, as amended, the term is more appropriately restricted to nonliving substances or compounds that are used for pest control. Biological control agents exhibit greater host or ecological specificity than most pesticides. While most biocontrol agents are highly host specific, others, such as antagonistic fungi, are effective against a variety of hosts. In nature, those that are host specific tend to adjust their numbers in response to fluctuations in the populations of their hosts. Nonliving entities lack these attributes.

The regulation of pest organisms by their natural enemies is ubiquitous; the more spectacular and best known examples involve introduced species that are severe pests until one or more of their natural enemies are added to the newly invaded region and effect some degree of control. Biological pest-control agents of this sort are usually well adapted to the environment occupied by the pest species and capable of self-perpetuation as long as suitable hosts are available. Biocontrol agents less well adapted to environmental conditions, where they are used, may still be effective if introduced into the ecosystem on a programmed basis or if environmental factors are manipulated to favor their survival.

Pests may also be controlled by use of individuals of the identical species made sterile or otherwise genetically modified so that when released in the pest's ecosystem they reduce the reproductive capabilities of their counterparts in the natural population. These biological agents have the advantage of being absolutely specific in their population regulation activities. Sterilized insects have an immediate repressive effect on natural populations. Certain types of genetic alterations, once introduced into a natural population, may persist and affect reproductive capabilities for several generations without the necessity for reintroduction.

This technical status report identifies problems, emphasizes the need for interdisciplinary approaches, and

outlines strategies for making practical use of biological control agents in pest management systems. The main thrust of the report is concerned with opportunities for use of biological control agents during the next several decades, specifically the kinds of biocontrol agents that have exhibited potentials, and with the research needed to resolve problems incident to their production and utilization. This look to the future requires an assessment of present knowledge and operational procedures, hence a synopsis of the current state of the art. This synopsis is intended only to provide perspective for future studies. Detailed considerations of the theory, philosophy, and principles of biological control are readily available in reference works (12, 70, 130).

An attempt has been made to arrive at general priorities for emphasis in different fields of study. The use of insects to regulate populations of other insect species, weeds, and some invertebrates is well established. Great strides have been made during the past decade in the autocidal method of population suppression. The use of pathogens and entomophagous insects for the regulation of insect populations, the use of pathogens for weed control, and the use of microorganisms for control of plant pathogens have considerable potential for commercial development. Although there are certain fundamental principles applicable to these fields of study, differences in the organisms themselves and in our levels of knowledge make it desirable that the various disciplines be individually appraised as to potential and patterns of development. This report has not addressed priorities <u>among</u> the various fields of investigation because, as knowledge expands, different perspectives as to potentially profitable lines of study will continue to emerge.

Another major objective of the study has been an appraisal of the consequences associated with the use of living organisms for pest control. Consideration of the relative benefits and hazards posed by various alternative methods in pest management is essential. Human safety and environmental impact are of prime concern. Different kinds of biological control agents will need to be evaluated by different sets of safety and efficacy criteria.

Significant progress in the use of biological pest-control agents will require a blend of theoretical modeling with knowledge gained from practical experience, including the testing of increasingly complex and comprehensive

combinations of management tactics. Attention must be directed to production methods and to manipulation of biocontrol agents in different combinations and in different situations to gain insight into how they should be used in coordination with other pest management practices. This approach will involve large-scale field trials as the most objective and practical method of testing management models.

Finally, consideration must be given to the public and private organizations, facilities, technical support, and information necessary to implement pest management programs that include use of biological pest control agents. Likewise, organizational coordination and cooperation must be sought if programs of regional or broader geographic scope shall succeed. It is hoped that this report will contribute to a synthesis of the technical, administrative, and social adjustments that will be necessary to utilize the advantages of biological methods of pest control for the benefit of the environment and mankind.

II. THE PEST SITUATION

Living organisms have the potential to increase their numbers indefinitely and to adjust their numbers in response to the dynamic environment in which they occur. These adjustments usually take place slowly without abrupt disruption of the network of living populations. Pest situations often arise as a result of environmental disturbances of an unusual nature or degree. Although catastrophic events--earthquakes, volcanic eruptions, hurricanes, floods--over which man has little or no control may induce pest outbreaks, man frequently generates his own pest problems as he strives to better his comfort and well-being. There are three common causes of man-generated pest outbreaks:

1) Introduction, either intentionally or accidentally, of potential pests into favorable environments without natural enemies being present;
2) Growth of susceptible crops or animals in essentially monoculture situations where host abundance allows buildup of larger pest populations; and,
3) Disruption through widespread and injudicious environmental manipulation and use of pesticides that adversely affect beneficial organisms and induce development of resistance and other changes in pest populations.

Pests occur in many forms--viruses, bacteria, and other types of microorganisms, fungi, weeds, nematodes, arthropods, mollusks, birds, and mammals. The methods chosen to cope with them depend upon the inherent nature of the pest and the types of environmental changes that permit them to become pestiferous.

The number of potential pests is virtually endless, and a meaningful estimate of the total number on a worldwide basis is impossible. This uncertainty exists largely because many normally innocuous species--those that are components of a "balanced" environment--have the capacity to become pests when their environment is disturbed in one way or another or when they gain access to a new region. Klassen _et al_. (141) estimate that the number of species known to reduce yields of crop plants includes at least 8,000 species of fungi, 10,000 species of insects or mites, and over 2,000 species of weeds; and Targan and Hopper (243) list some 2,000 species of nematodes. Approximately

10 percent of these pests are believed to be perennially important. In North America, about 700 species of arthropods are considered serious pests; of these, more than one-third have been accidentally introduced. Elton (83) has pointed out that we are living in a period of the world's history when the mingling of thousands of kinds of organisms from different parts of the world is setting up terrific dislocations in nature. Some of the resulting major biological explosions--the Hessian fly invasion of North America, the potato blight in Ireland, the spread of cactus in Australia, and the more recent rabbit disease in Western Europe--have helped alter the course of world history. The impact of contemporary ecological disruptions remains to be determined, although it is abundantly clear that many of our major pest problems have been caused by species that spread from their natural homes to other parts of the world. Some of these emigrant species, such as the cottonycushion scale, the Japanese beetle, and the weed St. Johnswort, have been amenable to a reasonable degree of control through the use of biotic agents; the feasibility of controlling others, such as the Hessian fly and the Dutch elm disease fungus, by the use of biotic agents has not yet been demonstrated. Against these latter pests, a different type of biological control, "host resistance," appears to be promising.

Potential pest species released from environmental constraints tend to show a characteristic pattern of increase and spread. The Japanese beetle is a good, well-documented example. When it was discovered in a nursery in New Jersey in 1916, the infestation involved less than 1 acre (228). During the next 7 years, the infested area increased to 3, 7, 48, 103, 270, 733, and 2,442 square miles. By 1920, within a radius of 5 miles of the site of original discovery, the average larval density of the pest had increased to 90,500 per acre; by 1924, average densities reached as high as 747,000 per acre. Limited areas showed larval population densities as high as 7,410,000 per acre (92). In subsequent years, the general population density trend was downward, although marked fluctuations in population levels occurred within the core area.

Endemic species, as well as adventive species that are under effective environmental restraints, often become pests as a result of environmental changes that favor them. The Colorado potato beetle and the boll weevil, both native to North America, became pests only after

extensive plantings of suitable food plants were geographically extended to touch their natural range. The southern corn leaf blight epidemic of 1970 was triggered by widespread planting of a susceptible crop--hybrid maize that carried the Texas cytoplasm for male sterility--coupled with growing season weather that favored development of the pathogen. Suppression of the natural enemies of the cottonycushion scale by chemical treatments in some citrus growing regions of California allowed a resurgence of that pest after it had, for many years, been under very effective control by biotic agents. The story of modern agriculture is replete with examples of pest situations that arose from the use of genetically susceptible crops or domestic animals, agricultural monoculture, and the trial and error approach with new crops and cultural practices. Although economic and social pressures may cause man to continue to risk the hazards of pest outbreaks, such potential hazards should be carefully assessed in advance.

Not all pests are uniformly amenable to various kinds of population regulating factors. Certain autocidal methods could be practical for use against species with high natural populations and high reproductive potentials. The sterile male method of population suppression is known to be effective with pests, such as the bisexual screwworm fly, that have low density populations. However, this method will not be effective against pests that reproduce parthenogenetically. Pests that are tolerated by their natural hosts may not have natural enemies that are sufficiently effective to prevent damage to more susceptible hosts. Examples are the tolerance of the Oriental chestnut and the susceptibility of European and American chestnuts to the blight fungus. Pest species such as the potato leafhopper, that have the ability to disperse great distances each growing season, presumably escape temporarily from whatever natural enemies occur in their permanent home; the seasonally invaded areas are less likely to have effective enemies in residence.

III. PRINCIPLES AND RATIONALE FOR THE USE OF BIOLOGICAL AGENTS FOR PEST CONTROL

The use of biological agents for pest control is based upon the premise that natural enemies of pests play major roles in regulating population levels. The degree to which the agents are effective depends upon a variety of factors. The inherent capabilities of the biocontrol agents are important, as are other factors that tend to repress pest populations, and whatever "management" tactics are invoked to favor the biocontrol agents. Biocontrol agents must work within the context of biological balance, and their success depends upon adjusting environmental conditions so that the desirable features are preserved, while the factors that inhibit the activities of biocontrol agents are avoided. This adjustment does not imply restoration of the identical conditions that prevailed before a pest outbreak occurred, but it does presume an understanding of the complexities of both the original and altered situations sufficient to identify the requirements of the biocontrol agents involved.

Both biotic and abiotic factors are involved in the broad concept of balance in nature. The physical characteristics of an environment--climate and soil and water composition--are the broad parameters that determine the general types of living organisms that can exist. Weather varies greatly in some regions and is narrowly circumscribed in others, contributing to the environmental stability or instability and hence to periodic changes in the composition of biota. If the abiotic forces remain stable for extended periods of time, the favored biota may by virtue of their own dominance change the environment so that it becomes less favorable; this permits other life forms to flourish. Thus, "balance" in the broad sense is a relative thing. It implies that forces or things exist at characteristic levels--in the absolute sense or in relation to other forces or things (129). Even an approximation of absolute stability for any extended period of time is improbable. Wherever life exists, things are in a state of flux.

It follows that in using biocontrol agents to ameliorate pest situations, the environmental parameters affecting natural enemies must be known in order to adjust environmental conditions to be detrimental to pests yet

favor biological control agents. For antagonists of soil-inhabiting plant pathogens, this may involve altering the pH of the soil or employing modified tillage methods (12, 31). For entomophagous insects it may be necessary to modify the plant community so that harborage, alternate non-pest hosts, and supplemental food sources will be available. Cultural practices designed to deplete pest populations may also deplete populations of their natural enemies unless knowledge of their interrelationships is available and taken into account. The concept of conserving natural enemies of pests is equally applicable to indigenous and established exotic species. The most important factors within the control of individuals (as contrasted to governments or organizations) are local environmental adjustments compatible with acceptable crop production practices and judicious use of pesticides.

The degree of specificity that exists in the pest and biocontrol agent interrelationship is an important consideration. For example, the nuclear polyhedrosis viruses of insects and the rust and smut fungi are able to replicate or reproduce in only one or a few very closely related host species. The most conspicuous successes in biological control have been achieved by agents that tend to be specific to the pest host. Such agents respond to changes in the population density of the host. However, if host populations are periodically depressed by other factors, the specific agent will suffer most, whereas a biocontrol agent that can adapt to other hosts will be able to maintain itself in the absence of a preferred host. When herbivores are used to control weeds, a high degree of specificity is essential to avoid damage to crop plants. There are many examples of habitat and behavioral specificity of entomophagous insects in certain host vegetative associations, even though the identical host species may be readily available elsewhere (245). The matter of specificity in biological control operations is discussed in considerable detail by Doutt and DeBach (80) and Baker and Cook (12).

Many pest situations occur as a result of the buildup of pest species in the absence of their natural enemies. Classical biological control--the introduction of exotic biotic agents--is particularly applicable in such situations. When exotic natural enemies are desired for use against an introduced pest species, where to search, what to introduce,

and whether all or only the best natural enemies are desirable, become important questions. Usually, the answer to the first question is in the country of origin of the pest. But species with pest potential are often opportunistic travelers, and the country from whence a given species was introduced may not be the country where it evolved. Even when the country of origin of a pest is not in doubt, the possibility of useful biocontrol agents from other regions should not be dismissed. By the same token, indigenous pest populations may be effectively suppressed by biocontrol agents with which they have had no prior association. For example, a hymenopterous parasite found in India shows great promise for control of the Mexican bean beetle in this country (56). Knowledge of the biology, systematics, and environmental requirements of the organisms usually guides the search (218).

Explorations for natural enemies usually disclose several species associated with the target pest. Any of the recognized kinds of biotic agents may be involved, and the utility and potential of each need to be critically appraised. In the past, efforts have been concentrated on searches for insects that are parasites or predators of invertebrates or for insects that feed on noxious plants. Parasites of insects may be primary, secondary, or cleptoparasitic in habit, and explorers experienced in such work usually readily discriminate among the species having different habits and concentrate on the primary parasites. All precautions should be taken to prevent introduction of potentially dangerous species. Safety and procedural guidelines pertaining to the utilization of biocontrol agents are discussed in this report under Resource Requirements and Developmental Considerations (Section V) and Considerations for Implementing Biological Control (Section VI).

A search for biocontrol agents usually reveals several that show potential and can be used without hazard to nontarget species. Often the several natural enemies found to attack a single host will have distinct preferences as to the stage or age of the host attacked. Some may be egg parasites, others larval parasites, and still others pupal or adult parasites. There are no reliable criteria for determining, *a priori*, which of several alternatives is "best."

There are many interacting aspects. For example, in the case of invertebrate pests, it might be multiple versus single species introductions; the relative value of parasites, predators, or pathogens; specific versus general predators and parasites. With parasitic insects, it might be the degree of synchronization with the target host, degrees of environmental tolerance, comparative fecundity, and searching ability. These aspects have been discussed in detail by Doutt and DeBach (80).

Classical biological control involves the introduction of biological control agents with the expectation that they will become established. However, not all useful biocontrol agents are capable of self-perpetuation where they are introduced and, even if they survive, may not be capable of suppressing pest populations. Thus, it may be desirable to manipulate populations of the biocontrol agents so that adequate numbers will be available at the optimum time. This tactic is referred to as augmentation. Application of antagonists to the soil for control of plant pathogens is a type of augmentation (12). Periodic application or distribution of pathogens of invertebrates is another useful practice. Although the value of the augmentive method involving periodic releases of entomophagous arthropods to supplement those populations already present is still being discussed, the additional discovery of synthetic and natural chemicals that influence behavior of the arthropods and the increased proficiency in mass producing biocontrol agents will make this approach even more promising (148, 205, 237).

In situations where the biocontrol agent cannot survive during certain periods due to climatic conditions, cultural practices, or other causes, the release of relatively small numbers of biocontrol agents at a time when the environment is favorable or when suitable stages of the pest host are available has proven a valuable practice in pest control. Examples include release of a hymenopterous parasite for control of the Mexican bean beetle (235) and the release of other parasites and predators to control pests in greenhouses (131).

In summary, the rationale for using biological control agents is to reduce populations of the pest to prevent economic damage. Only rarely do these agents eliminate a pest from a given site, for example, when the sterility

method is used for population eradication. Eradication, generally is not the objective because, in most cases, the survival of biocontrol agents depends upon survival of their hosts in the ecosystem. It is also essential to recognize that regulation of the spread and activity of a biocontrol agent, once introduced and established, may not be possible. Finally, the specificity of biocontrol agents for particular hosts is an important factor in developing a reasoned approach to use of biocontrol agents.

IV. BIOCONTROL AGENTS, THEIR NATURE AND ECOLOGICAL PROPERTIES

"Great fleas have little fleas upon their backs to bite 'em,
And little fleas have lesser fleas, and so ad infinitum.
And the great fleas themselves, in turn, have greater fleas to go on;
While these again have greater still, and greater still, and so on."

--Augustus De Morgan,
A Budget of Paradoxes.

Biological control agents, like pests, occur in a great variety of forms. Those considered in this report are grouped, for convenience of discussion, in six general categories: Vertebrates, arthropods (spiders, mites and insects), nematodes, snails and other invertebrates, microrganisms (pathogens that affect invertebrates, plant pathogens and microbial antagonists), and higher plants.

VERTEBRATES

Vertebrates, both carnivores and herbivores, play significant roles in the control of pest populations. They are important largely in stabilizing population levels rather than in lowering them to nonpestiferous densities. Unfortunately, quantitative data adequate to assess the importance of most species are usually not available. Furthermore, because most vertebrates, particularly birds and mammals, have behavioral patterns far more complex and adaptable than those of invertebrates, they tend to be opportunistic feeders and may neglect pest populations if other acceptable food sources are readily available.

Although insectivorous birds that inhabit suburban communities, diversified farming regions, and forests contribute to pest control, their actual impact on the ecosystem is difficult to determine. Similarly, the value of flocks of gulls that prey upon white grubs during spring plowing of farmlands or feed on crickets and grasshoppers during outbreaks should not be discounted. But, in the light of past experiences, introduction of birds for purposes of controlling pests seems inadvisable. The Indian mynah was successfully introduced into Mauritius to control

a locust; but the same species introduced into the Hawaiian Islands and Australia has become a pest, and its value in those regions is equivocal. The starling appears to be a useful bird in regions where its population remains low, but in both Great Britain and the United States it is definitely a pest. Displacement of native bird populations, flocking habits, and urban roosting behavior make such species locally objectionable even though they may exercise a degree of pest control in certain situations.

Management of potentially useful bird species consists primarily in providing suitable nesting sites and cover to encourage their presence in areas where and when pests occur. However, the territorial behavior of most bird species limits the resident population that can be attracted by such actions during the breeding season, when food consumption is high and pests most abundant. Domestic ducks and geese are sometimes used for weed control in many situations (261) and the former are useful in keeping down populations of noxious snails (263).

Among the mammals, bats, mice, and shrews are probably the most effective insectivores. As with birds, there is little solid evidence of the impact of bats on pest populations. In areas where bats are abundant, they consume enormous quantities of insects, judging from the abundance and contents of feces in their roosting places. Shrews and mice appear to have considerable value as biocontrol agents where they feed on pests in forest habitats. One species of shrew (Sorex cinereus) was introduced into Newfoundland from the adjacent continental area and was successful in depressing populations of the larch sawfly in a climax coniferous forest environment (246). The mouse (Peromyscus leucopis) has been shown to be an important predator of the gypsy moth in New England (39). Another mammal actively studied for weed control in the past is the manatee (20).

Reptiles and amphibians appear to have limited utility in pest control. Lizards account for a considerable mortality of insects, some of which are pests, but their effects on pest population dynamics are not documented. The giant American toad (Bufo marinus) and the European toad (B. bufo) appear to be effective in certain habitats. The former has been shown to be useful against coleopterous pests in sugarcane fields (76), and the latter is used to control pests in greenhouses.

Of all the vertebrates, fish are undoubtedly the most useful for the control of pest insects, particularly mosquitoes and midges (45, 97). Numerous species are known to be insectivorous, but the management of fish for mosquito and midge control has been limited primarily to the mosquito fish and the guppy. The use of these two species, and a few others, for control of mosquito breeding in shallow waters and artificial containers is widespread in warmer parts of the world. Unfortunately, the mosquito fish shows some tendency to be selective in its feeding, and may not always be effective in suppressing malaria vector populations if larvae of preferred species are readily available. Neither fish is suitable for human food.

In some situations herbivorous fish such as Tillapia, Ctenopharyngodon, and Cyprinus species are useful in aquatic weed control in rice paddies and artificial fish ponds (8, 248). Fish of these genera, carp for example, provide food for man; but efficient use of them in a dual role requires considerable management knowledge and skill. Indiscriminate introduction of presumably useful species of fish should be avoided, as with birds, and all introductions should be preceded by critical ecological studies.

In summary, relatively few vertebrates are amenable to management for control of pest populations, although many species, through their natural behavior, undoubtedly play significant roles in keeping pests at low levels. Woods (263) has provided a useful account of vertebrates as pest control agents.

ARTHROPODS

As a group the arthropods unquestionably predominate both in the numbers of kinds that are pests, and the numbers that play important roles in regulating populations of other animals. The importance of insects as biological control agents is particularly noteworthy, as evidenced by the numerous treatises that deal with their use in biological control programs (for example, 70, 72, 127, 130). In fact, development of principles and practices in the field of biological control derives in large part from studies of insects as natural enemies of insects. Except for

insects and mites, the roles of other arthropods as regulators of pest populations are little known. Within the limits of their rather specialized environments, centipedes and scorpions and their relatives play an important part in maintaining a balance of animal life, but as a group are more likely to be regarded as pests of humans than as benefactors. Only the common house centipede, which feeds upon small animals that share its habitat, has any significant reputation as a pest control agent. A list of arthropod parasites and predators imported for control of insect pests and weeds, with estimates of their efficacy, is available (156).

Spiders and Mites

Spiders, all of which are predators, occupy an equivocal position. Most are opportunistic feeders, but a few are selective feeders (263). Some may be classed as pests because of their destruction of beneficial insects; others, particularly those that inhabit vegetation and feed upon herbivorous insects, are beneficial, although the benefits are more as general population regulators than as enemies of pest species. In Japan, spiders are thought to be important in early season control of leafhoppers in rice fields. However, at present, spiders are not amenable to "management" for use as biotic agents because mass rearing techniques have not been developed. The best tactics for maximum exploitation of them would be maintenance or creation of environments (absence of toxic chemicals) that permit their survival.

Mites are important as regulators of pest populations. Predatory species of *Typhlodromus* and *Phytoseiulus* have been shown to be effective in regulating populations of several species of spider mites that are serious pests of cultivated crop plants (132). Because these predatory mites are not so vagile as the spider mites, which disperse by "ballooning," they cannot regularly be depended upon to regulate populations of their prey; augmentation or re-introductions in pest-occupied habitats may be required. However, inasmuch as spider mite outbreaks appear to be triggered by injudicious use of chemical pesticides that eliminate the predatory mites, a reasonable level of natural spider mite control may be possible in the absence of pesticidal applications or by selective use of pesticides.

Numerous trombidiform mites are predators of insects and other mites, for example, Allothrombium fuliginosum, a predator of eggs of the European corn borer, Cheyletus spp. that prey on tyroglyphid mite pests of stored products, and Macrocheles muscaedomestica that preys on eggs and first instar larvae of the housefly. The last mentioned species seems to have considerable potential for control of fly breeding if suitable environmental management practices are followed with the breeding medium, animal dung (9).

Although serious work directed toward "management" techniques for mites as biotic agents for pest control has only recently begun, the outlook is promising (57). Predatory mites of some kinds disperse by attachment to the mobile stage of their host (phoresy), but in general it would seem that their value could be increased by distribution as needed. A red spider mite, Tetranychus desertorum, probably contributed to some extent to the biological control of cactus in Australia; the possibility of using phytophagous mites for the control of weeds is being critically investigated.

Insects

Insects may be used as biotic agents for pest control in three basically different ways: As parasites or predators that attack their animal hosts (the pest species), as herbivores that feed on noxious plants, or as genetically modified populations that affect the reproductive potential of "wild" populations of the same species. Although some common features apply to all three methods, it is convenient to consider them separately. Relatively few species have been shown to be amenable to genetic modifications that make them effective control agents, but the number of potentially useful parasites, predators, and herbivores is legion. For example, in a single hymenopterous family Ichneumonidae, all members of which develop as parasites of other insects, Townes (244) estimated that there are 60,000 species in the world, yet only about 16,000 of these have been named. Our knowledge is equally fragmentary of the world's fauna in other groups of prime importance as biotic agents for pest control. Clausen's monumental treatise on entomophagous insects (48) includes discussions of representatives of 224 families in 15

(or 16, depending upon the classification followed) orders that have adopted, in some measure, the entomophagous habit. Clausen (48), Balduf (14), and Askew (7) provide a wealth of information about the anatomy, biology, and habits of entomophagous species. Insects are also useful for the control of invertebrate pests other than arthropods, particularly snails.

Entomophagous and Phytophagous Insects. The role of many parasitic and predatory insects is in maintaining a balance among the organisms within the environment they occupy. This is a most important role because it prevents those of their hosts that have the potential to become pests from doing so. Many others, even though voracious feeders, may have little effect on population levels of their prey because they are too opportunistic in their feeding habits or too few in numbers. Dragonflies, that feed on mosquitoes and midges and mantids and scorpion-flies, that feed on many kinds of small insects, are in this category. Although a few entomophagous species in other insect orders are useful as pest control agents, this report considers primarily those belonging to the Hemiptera (true bugs), Coleoptera (beetles), Neuroptera (lacewings and others), Diptera (two-winged flies) and Hymenoptera (ants, parasitic wasps, and others).

Insects are the largest group of natural enemies of weedy plants, and host-specific insects have been used in the biological control of weeds for over 100 years. Their value has been demonstrated in many countries, and insects are now under study in over 70 weed control projects in North America alone. They have proven of greatest value against introduced weeds. The weediness of some introduced plants may be partially attributed to the absence of natural enemies in their new habitat. The search for, testing, and introduction of exotic biotic agents for control of these weeds is often an attempt to correct this imbalance. Weed-feeding insects have been used primarily to control perennial or biennial species growing in areas of low disturbance such as rangeland, forest, and pasture. Unfortunately, a high degree of disturbance (for example, cultivation) frequently interrupts the insect developmental cycle, precluding their increase to control levels in cropped or similarly disturbed areas. Most of the phytophagous insects thus far used for weed control

belong to the orders Hemiptera, Lepidoptera, Coleoptera, and Diptera; occasionally insects of the orders Thysanoptera, Orthoptera, and Hymenoptera are used.

Grasshoppers are usually considered to be pests, but some are specific enough in their habits to warrant use as agents for weed control. One leaf-feeding species from South America, *Paulinia acuminata*, has been introduced into Africa to help combat the floating aquatic fern, *Salvinia molesta*, in Lake Kariba. *Salvinia* is a serious aquatic weed in parts of Asia and Africa, where it is naturalized from the neotropics (3).

Among the Hemiptera, some of the more useful species belong to the family Miridae, which are primarily plant feeders. However, some are facultative predators. *Tythus mundulus* is an effective control agent for the delphacid sugarcane pest, *Perkinsiella saccharicida*, in Hawaii because it feeds upon the eggs deposited in plant tissue. A related mirid *Cyrtorhinus fulvus* has been used with substantial success for control of a different delphacid, *Tarophagus proserpina*, in some of the islands in the Pacific. Still another mirid, *Blepharidopterus angulatus*, is one of the most effective predators of fruit tree red spider mites in Great Britain (263). Other useful predatory Hemiptera occur in the families Pentatomidae, Reduviidae, Anthocoridae, Lygaeidae, Nabidae, and Coreidae. Numerous species of Anthocoridae are of particular interest because they prey upon phytophagous forms such as spider mites, aphids, scale insects, and small caterpillars. Two species of *Geocoris* (family Lygaeidae) are considered to be important as part of the total predator complex that preys upon aphids on sugarbeet, potato, and pea crops in the Yakima Valley of Washington (242).

A leaf-feeding bug, *Teleonemia scrupulosa* (family Tingidae), is the most important of the complex of insects introduced into Hawaii for control of *Lantana camara*, a noxious range weed originally brought to Hawaii in 1885 as an ornamental. Early season feeding by *Teleonemia* combined with winter defoliation by three species of leaf-feeding Lepidoptera has provided substantial control of the weed. The cochineal insect, *Dactylopius coccus*, is a most effective natural control agent for cactus on over-grazed rangelands of the Santa Cruz Islands off the coast of southern California (5).

Phytophagous thrips have also been used as biological agents for weed control. *Amynothrips andersoni*, along with a fleabeetle and a stem-mining Lepidoptera, is being used to combat alligatorweed in the United States (230).

The Neuroptera include some 19 families, all members of which are predaceous, at least in the larval stages. Some members of two families, the green lacewings (Chrysopidae) and the brown lacewings (Hemerobiidae) are important biological control agents, although, thus far, only some of the green lacewings have been widely used in the sense of being manipulated. The larvae of green lacewings are predators of aphids, small lepidopterous larvae, other small soft-bodied insects, and spider mites (203). The adults of some species are also predators.

Those species of green lacewings that feed on honeydew as adults can be manipulated to concentrate populations in specific areas by using artificial "honeydew" consisting of mixtures of yeast hydrolysates, sugar, and water (104). Some species of *Chrysopa* are being mass produced in the laboratory and are available for sale as agents for pest control.

The brown lacewings are predaceous on aphids, mealybugs, mites, and various kinds of insect eggs. Thus far little use has been made of species in this family because of the lack of information about their biologies and ecological requirements. However, recent studies indicate that brown lacewings can develop at very low temperatures (0.4-4.1^{o} C), suggesting that they may be useful for very early season control of aphids when other kinds of biological control agents are not yet active (187, 188).

The importance of Lepidoptera as agents for pest control results from their primarily phytophagous habits in the larval stage. Larvae of Lepidoptera are the most important insects that feed on the dwarf mistletoes, at times causing severe damage to external parts of the plants (236), and the use of insects offers considerable promise for control of these important plant parasites (112). A moth, *Cactoblastis cactorum*, with an associated bacterium that invades plant tissue following feeding of the moth larvae, is largely credited with the spectacular control of cactus (*Opuntia* spp.) in Australia. Larvae of the

cinnabar moth, _Tyria jacobaeae_, are the most important biological agents yet evaluated for combatting the poisonous weed tansy ragwort (_Senecio jacobaea_) in pastures and rangelands of northwestern California, Oregon, and Washington. Three species of defoliating Lepidoptera are important supplemental agents in use against lantana in Hawaii, and a stem-mining moth, _Vogtia malloi_, is an important agent in alligatorweed control in the southeastern United States (4).

The Coleoptera, here construed as including the Stylopidae which are often treated as a separate order (Strepsiptera), probably contain the majority of all insects of predaceous habit. The Stylopidae are parasitic and are undoubtedly useful in regulating populations of pestiferous leafhoppers and delphacids but are not amenable to manipulation because of their complex biologies. Carabidae (ground beetles) are considered to be important in control of lepidopterous pests and one species, _Calosoma sycophanta_, is believed to be one of the important enemies of the gypsy moth in the Eastern United States (50) where it has been established.

The lady-bird beetles (Coccinellidae) are the most important of the Coleoptera as biotic agents for suppression of pests. They have been particularly useful for control of scale insects and mealybugs and to a somewhat lesser extent for aphid control. Members of one genus, _Stethorus_, feed on mites. The famous vedalia, introduced to North America to control the cottonycushion scale, is a coccinellid.

Most Coccinellidae are capable fliers and able to move about in search of suitable hosts. In fact, the tendency to disperse or migrate from areas where hosts are not available sometimes lessens their effectiveness in preventing pest outbreaks. Some species, like _Hippodamia convergens_, exhibit a consistent pattern of aggregation in the mountains in the winter and migrate from the mountains to lower elevation in the spring. These changes in flight patterns are determined by the physiological condition of the insects and the weather, and they are difficult to alter. Some success has been achieved by using food sprays (artificial honeydew) to retain beetles in the desired area. These sprays provide the necessary protein to induce oviposition when prey populations are insufficient to do so (104).

The reproductive capacity of Coccinellidae is relatively high, although the rate of development from egg to adult is not sufficiently rapid to permit beetle populations to quickly overtake a population explosion of a rapidly reproducing prey such as aphids. Fortunately, most adult beetles utilize the same prey as the larvae, although perhaps favoring a different developmental stage of the prey, and this compensates somewhat for the lag-time in population increase of the predators.

Numerous other families of beetles contain entomophagous species, but few have been specifically used as biotic agents. Balduf (13), and Clausen (48) should be consulted for a comprehensive account of the entomophagous habit in the Coleoptera.

Phytophagous beetles are some of the most important biological agents used for the control of weeds and were the agents of choice in the first attempt at biological control of a weed in the United States. Chrysolina quadrigemina and C. hyperici, both leaf-feeding Chrysomelidae, were introduced into the Western United States in 1945-6 to control the poisonous weed Hypericum perforatum that then infested some 2.3 million acres of rangelands in California alone. Within a very short time the weed was effectively controlled, primarily by C. quadrigemina, and now remains at a level of less than 1 percent of its former abundance in California.

Another defoliating chrysomelid, Agasicles hygrophila, was introduced from South America in 1964 to combat the aquatic alligatorweed, Alternanthera philoxeroides, which then infested some 97,000 acres in eight States from Texas to North Carolina and seriously hindered navigation and other water uses. Damage to the plant by this beetle and two other introduced agents has resulted in a drastic reduction of alligatorweed abundance (3, 230). Members of other families of phytophagous beetles have been used as weed control agents, particularly the weevils (family Curculionidae), which are being used to control thistles (151) and other weedy plants.

Dung beetles (family Scarabaeidae) are being utilized in the control of flies that breed in dung, by habitat elimination, and in "control" of the dung itself (256).

There is a remarkable diversity of habits amongst the entomophagous Diptera (two-winged flies), and the order contains many species that are important in the biological control of pest species of insects. The great majority of the parasitic species are primary parasites of plant pests and markedly beneficial. Although some Tachinidae attack honey bees and spiders, as a whole the members of the family are beneficial. Other families which include parasitic species, such as the Bombyliidae and the Sarcophagidae, occupy an equivocal position because many are harmful while others are beneficial. Still others, such as the Nemestrinidae and the Pipunculidae, are all beneficial so far as known. Among the predaceous families, the hover flies (Syrphidae) contain numerous species that are beneficial because they prey upon aphids, scale insects and related Homoptera. Clausen (48) and Askew (7) provide more detailed information on the many families of flies that exhibit predaceous or parasitic habits.

The larvae of some species of Syrphidae are predaceous on pest species of phytophagous insects, primarily aphids, but also jumping plant lice, certain kinds of scale insects, spittle bugs, and small caterpillars. Although they undoubtedly play an important role in reducing pest populations, solid evidence that they are reliable and effective biocontrol agents, except in specialized situations, appears to be lacking. They are not readily manipulated, and seem most useful as components of diversified environments where they help maintain a natural balance.

All known species of Cryptochetum (family Cryptochetidae) are internal parasites of Homoptera (Margarodidae). The best known species, C. iceryae, introduced from Australia, is an effective parasite of the cottonycushion scale, Icerya purchasi, and probably would be much better known as a biological agent were its activities not overshadowed by the spectacular performance of the vedalia.

Members of the families Anthomyiidae and Sarcophagidae are undoubtedly important as natural enemies of grass-hoppers and locusts, the former as predators of egg capsules, the latter as parasites of either nymphal or mature hosts (201). Their importance in suppressing populations of pest species is not well documented, although

one species of Sarcophagidae, Wohlfahrtia euvittata, is at times sufficiently effective against swarms of Locustana in South Africa to be responsible for discontinuation of locust poisoning programs. Sarcophaga kellyi has been reported to be similarly effective against swarms of Dissosteira in southwestern United States. Both these species oviposit on adult locusts in flight.

Undoubtedly, the Tachinidae is the most important family of flies for effectiveness as biocontrol agents against crop pests. Many species of many genera parasitize such important crop pests as lepidopterous larvae, larval or adult beetles belonging to several economically important groups, and members of the hemipterous families Pentatomidae, Pyrrhocoridae, and Coreidae. Centeter cinerea kills about 90 percent of the adult Japanese beetles in northern Japan when populations of that species are high and is presumed to be responsible for keeping the pest under control. Winthemia quadripustulata is important in suppressing armyworm populations in North America, and Trichopoda pennipes is similarly effective against squash bug populations and some stink bugs. Lixophaga diatraeae, Paratheresia claripalpis , and Metagonistylum minense parasitize lepidopterous larvae that bore in stalks. These parasites show considerable promise as agents for control of the sugarcane borer (146). Several tachinids are also important parasites of the gypsy moth (215).

Marsh flies (Sciomyzidae) are either parasitic or predaceous on land and aquatic snails, and to a lesser degree, on slugs. Sciomyzidae that are natural enemies of snails that are intermediate hosts for helminths parasitic on man and other animals may eventually be used in the biological control of these parasitic diseases (105).

Some Diptera are useful in weed control. A seed fly, Hylemya seneciella, has been introduced into the United States to help combat tansy ragwort, and a gall fly, Procecidochares utilis, was imported into Hawaii to control pamakani, Eupatorium adenophorum. The former destroys developing seed heads; the latter, by galling the plant stems, reduces their length and foliage production to such an extent that the host weed is no longer an effective competitor (5). Several other anthomyiid, tephritid, and cecidomyiid flies have been useful in weed control.

In general, Diptera are highly vagile and thus, they are able to seek out pest population outbreaks and, if necessary, move with mobile swarms of pests such as migratory locusts. Without their suppressive action many pest species would undoubtedly become much more serious. Unfortunately, few of the more effective species of flies are amenable to being managed in the sense that they can be readily propagated en masse, or to having their behavior manipulated sufficiently to assure maximal effectiveness. At present, the principal methods employed for optimizing effectiveness of flies as biotic agents are in the general category of environmental manipulation, that is, providing supplementary food sources, harborage for adults, and pupation sites. These are undoubtedly the most practical means available to individual growers.

The Hymenoptera are unquestionably the dominant order among the entomophagous insects, both in the number of species having that feeding habit, and in the frequency and effectiveness with which they attack insect pests of agricultural crops and forests. According to Clausen (48), about half the families having entomophagous representatives are strictly parasitic, one-fourth are predaceous only, and the remainder contain both parasitic and predaceous species. Askew (7) estimated that the Hymenoptera contain 100,000 parasitic species. The Ichneumonidae and Braconidae attack a wide variety of caterpillars and sawfly larvae, also adults and larvae of beetles. The Encyrtidae and Aphelinidae are usually parasites of Homoptera, but some Encyrtidae also attack Lepidoptera, Coleoptera, and ticks. The Scoliidae and Tiphiidae parasitize grubs of the beetle family Scarabaeidae. Trichogrammatidae, Mymaridae, and Scelionidae are egg parasites. The ants, Formicidae, are the most important of the predaceous groups. Some Hymenoptera, for example, the sawflies, are phytophagous and may have value as weed control agents.

There is a fantastic diversity in the biologies of the various entomophagous species in this order, which contains most of the biotic agents routinely used in biological control actions. Among other highly specialized behavioral traits that make egg parasites among the Hymenoptera effective biotic agents is phoresy, a trait not uncommon amongst those species whose hosts lay their

eggs in masses (51). In some groups, some species are parasitic, others predaceous, and still others phytophagous, for example, species of *Eurytoma*. Some species have developed into secondary parasites (hyperparasites), that is they are parasites of a parasite. For example, a species of *Lygocerus* is parasitic on a species of *Aphidius* which is parasitic on an aphid. This habit is found only in the Hymenoptera. The development of complex biologies is common in certain groups, such as the Aphelinidae. A species of *Encarsia* parasitizes whitefly nymphs if the ovipositing female has mated, but if she is a virgin she will parasitize eggs of noctuid moths. In this case mating has the effect of altering the behavior of the female and changing the parasite-host relationship. Adult parasites in general do not depend on their host for food, but among the Hymenoptera, females of many species feed as adults on the host which they frequent, causing high mortality. For example, *Metaphycus helvolus*, a parasite of the black scale, *Saissetia oleae*, may cause higher mortality as a result of adult females feeding on the host than as a result of parasitization. Knowledge of the complex biology of parasitic Hymenoptera is essential for the successful manipulation of these species for pest control.

The preponderance of successes in classical biological control projects probably can be attributed to Hymenoptera (70). Two species of parasites, *Allotropa burrelli* (Platygasteridae) and *Pseudaphycus malinus* (Encyrtidae), are credited with giving complete control of the Comstock mealybug on apple in the Eastern United States. Another platygasterid species, *Amitus hesperidum*, together with *Eretmocerus serius* and some species of *Prospaltella* (Aphelinidae), has provided control of the citrus blackfly in Cuba and Mexico. *Aphytis holoxanthus* (Aphelinidae) is credited with control of the Florida red scale of citrus in Israel, and *Aphelinus mali*, another aphelinid, gives complete control of the woolly apple aphid in New Zealand. *Campsomeris annulata* (Scoliidae) gives complete control of a beetle pest of sugarcane, *Anomala sulcata*, in the Philippines. The aphelinids, *Aphytis maculicornis* and *Coccophagoides utilis*, have completely controlled the olive scale, *Parlatoria oleae*, in California. The walnut aphid, an important pest in California, has been controlled by a strain of *Trioxys pallidus* imported from Iran.

A complex of imported and native predators, together with disease organisms, is credited with substantial control of the spotted alfalfa aphid. Many hymenopterous parasites have the ability to disperse over considerable distances, thus making them particularly useful against highly mobile pest species such as the spotted alfalfa aphid. However, some parasites that lack mobility may still have the capacity to be effective agents for pest control. One such is *Neodusmetia sangwani*, which parasitizes the Rhodesgrass scale, and successfully controlled that species in south Texas after being widely distributed by airplane releases (221).

Spalangia endius (Spalangiidae), a parasite of the pupal stage of house flies, has been shown to have the ability to suppress housefly populations when mass produced and released in a sustained fashion (182). Another hymenopterous parasite, *Aphidius smithi*, has been propagated *en masse* in portable field cages in alfalfa fields for release at appropriate times to parasitize pea aphids in adjacent pea fields in the Pacific Northwest (106). Parasites of scale insects are also propagated in the insectary in large numbers for inoculative releases (72). Predaceous wasps that prey on larvae of Lepidoptera cause significant reductions of hornworm populations when colonies are concentrated in or near tobacco fields (158). Many other successes have been achieved by Hymenoptera of diverse families (70).

One area that shows promise in augmenting biological control agents, particularly the parasitic Hymenoptera, is the behavioral manipulation of parasite populations through the use of kairomones. The importance of behavior in host location and selection is discussed by Vinson (253), and the potential for the use of this information in manipulating parasite populations for control is described by Lewis *et al*. (161).

In summary, the Hymenoptera are extremely useful in biocontrol of insect pests, particularly pests of agricultural crops and forests. They are generally amenable to propagation in large numbers, and to manipulation in the sense of shipment for release and handling in insectaries. The highly developed nervous system of hymenopterous insects, reflected by their complex behavior patterns, suggests that once their responses to the

chemical messages of their environment are better understood, they will be even more susceptible to management and manipulation as biotic agents.

Autocidal Methods. Members of a species may be modified and manipulated so that they lower the reproductive or survival potential of naturally occurring populations of their own kind. Well-documented accounts of autocidal methods of pest control are given by Woods (263), Fitz-Earle (91), and Knipling and Klassen (149). Several methods have been proposed and tested: Sterilization by ionizing radiation or chemosterilants, cytoplasmic incompatibility, chromosomal translocations, introduction of deleterious or fully lethal genes, and hybrid sterility. Although these differ in certain fundamentals, they have in common some basic requirements for practical application; namely, that the target pests reproduce bisexually and that there is a thorough understanding of their biology, ecological requirements, and behavior.

By far the best known of these so-called autocidal methods is the sterile-male technique (18, 142). Theoretically useful for suppression of a great array of bisexually reproducing organisms, its practical application has thus far been limited to use against insect pests. In this method, large numbers of sterile insects--in most cases males only, but sometimes both sexes when sterility is complete--sufficient to greatly outnumber the resident wild population are released. A calculated proportion of 10 or more sterile to 1 fertile insect is usually attempted. If the sterile insects are fully competitive in mating and longevity, a downward trend in the total population level will be initiated. If the release rate of sterile insects remains constant and occurs at appropriate intervals of time, the probability of fertile matings in the population will markedly decrease. Both the absolute and proportionate numbers of fertile individuals will further decline, with population extinction occurring in about four generations of the pest species, assuming effective distribution of released insects and no infiltration of fertile individuals from adjacent areas. Knipling (142) has provided mathematical models to illustrate the population decline that may be expected.

The practicality of this method has been amply demonstrated by eradication of the screwworm fly from the Southeastern United States (143), and its use in maintaining

populations of the pest at low levels in the Southwestern United States and adjacent Mexico by annual releases of 8-10 billion sterilized flies. Other uses of the technique involve the use of sterilized moths of the pink bollworm, released in the San Joaquin Valley, California, each cotton-growing season since 1967 (147). The releases are designed to prevent the establishment of the pest in the important cotton-growing area. Moths in low numbers spread into the San Joaquin Valley each year from heavily infested cotton grown in the Imperial Valley, California, and from Arizona. This program involves the mass production, sterilization, and release of about 100 million moths each year. As yet, it is not possible to prove that this suppressive measure alone, or other measures that have been used, are responsible for the absence of established pink bollworm infestations in the San Joaquin Valley, but all criteria available for measuring results indicate that the program is achieving its objectives.

In a similar program, sterilized Mexican fruit flies have been released annually in southern California since 1964 to prevent the establishment of this major pest of fruits and vegetables (223). Small numbers of this insect move into California from infestations originating in Tijuana, Mexico. The release of these sterile insects has replaced the use of preventive insecticide applications. Sterilized Mediterranean fruit flies have recently been employed as a supplement to chemical sprays to eliminate an established infestation of that pest found in Los Angeles, California, in 1975. Other trials of the sterile insect method in the United States, resulting in good suppression or elimination of circumscribed natural populations, have involved populations of several pest species, namely, the boll weevil, codling moth, oriental fruit fly, melon fly, Caribbean fruit fly, cotton bollworm, horn fly, stable fly, and certain species of mosquitoes.

Different kinds of insects vary greatly in their susceptibility to radiation. Gamma radiation from ^{60}Co sources is usually preferred, but numerous chemical compounds that induce sterility in insects have also been tested in varying degrees against a broad spectrum of pest species (155, 263). In general, species of Diptera have been most amenable to sterilization. Lepidoptera, as compared with most other insects, require larger doses of radiation to effect sterility (191). Because complete sterility of moth species could not be accomplished without associated

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debilitating effects that would limit their usefulness, partially sterilized populations of moths have been used in some pest control programs. Due to the phenomenon of inherited sterility in Lepidoptera, there would be some unique advantages in using this tactic (145, 191).

Suppression of pest populations by the cytoplasmic incompatibility method requires the use of different strains of the target pest that mate readily but fail to produce viable progeny because the male sperm does not fuse with the egg nucleus, although meiosis is stimulated by the sperm entering the egg. This sort of mating incompatibility is known in several kinds of insects but has been studied as a population suppression method primarily in the mosquitoes.

Hybrid sterility has been demonstrated in a number of insects, but specific efforts are being made to utilize the hybrid sterility resulting from the interspecific crosses between two lepidopterous species, *Heliothis virescens* and *H. subflexa* (157, 199). Very recent studies in Mississippi indicate that the hybrids are competitive with native *H. virescens* moths and may prove useful in population suppression.

The full potential and practical utility of such genetic methods as cytoplasmic incompatibility, hybrid sterility, chromosomal translocations, and the use of deleterious or fully lethal genes for pest population suppression must await the accumulation of more basic information about insect genetics and a critical assessment of the operational procedures that will be involved. Current knowledge regarding these methods is summarized by Woods (263) and Whitten and Foster (259). The relative efficiency of the various genetic methods is discussed by Knipling and Klassen (149). Any of the methods that adversely affect the reproductive or survival capabilities of pest insects in the natural environment have obvious value. Such possibilities include inability to diapause, reduced fecundity, sex ratio distortion, reduced mobility, asynchrony in seasonal development, and others. However, as Whitten and Foster (259) point out, theory currently far outstrips practice in the implementation of genetic approaches to insect control, other than in the sterile-insect release method.

The use of autocidal methods for biological control has certain advantages and problems. The autocidal method is absolutely specific to the target pest, and those tactics

that involve releases of large numbers of altered insects, for example, sterile males or those that exhibit cytoplasmic incompatibility toward females of the wild population, have the unique property of becoming increasingly effective as the resident wild population declines, so long as the rate of releases remains constant. The ability of insects to find mates, so essential to population survival when numbers of individuals are low, becomes a disadvantage to a population subjected to sterile insect releases. Thus, the method may be especially useful for eradication of incipient or low-level infestations or to prevent low-level populations from reaching economically important levels.

Practical use of autocidal techniques requires that the following important conditions be met (144):

1) Suitable methods of sterilizing or genetically altering insects without changing their normal behavior or vigor, particularly as these characteristics concern mate finding and mating.
2) Availability of efficient and economical rearing methods for those tactics that involve massive releases of modified insects.
3) Reliable information regarding the population dynamics of the target pest, including quantitative information on the number and distribution of the natural population, as a guide to the number of altered insects needed in various parts of the pest's ecosystem. Initiation of autocidal methods should coincide with the predetermined low ebb in the natural pest population.
4) Efficient methods of handling and releasing the propagated insects.
5) Insects to be released that are not capable of causing annoyance or damage; if they are capable of doing so, the numbers released must be kept within tolerable limits. If chemosterilants are used on released or wild populations, there must be assurance that residues of the sterilant do not become environmental pollutants.

In summary, the principles of pest population suppression by autocidal methods are sound, and the technique provides new dimensions in pest suppression technology when used to supplement or complement other pest control methods. Under some circumstances the technique is practical when used alone, but its greatest potential is as a component in a coordinated pest management program.

NEMATODES

The association between nematodes and insects varies from benign phoresy to obligate parasitism (100, 197). Certain parasitic nematodes are effective biological control agents for suppression of insect pests.

Nematodes are one of the major biotic factors affecting bark beetle populations. For the most part, life histories of the parasites are synchronized with their host. Adult parasites are usually produced in adult beetles. Many of the parasites sterilize their host. It may be possible to sterilize one or both sexes of a given beetle population by the planned introduction of nematode-infested beetles, or by altering the life history of a parasite so that mature nematodes are produced in immature beetles (173).

The first nematode to be used for insect control, *Neoaplectana glaseri*, caused high mortality in populations of the Japanese beetle in New Jersey (98). More recently, another strain of this nematode has been used experimentally against a wide range of hosts, including the codling moth, the Colorado potato beetle, and the whitefringed beetle. Recently another nematode *Romanomermis culicivorax* (=*Reesimermis nielseni*), has been used against mosquitoes.

Augmentation of nematode populations for biological control requires mass culture procedures, preferably through use of *in vitro* techniques, which are currently unavailable. The successful rearing techniques developed for the several neoaplectanid species and mosquito parasites lend confidence that with additional research, mass culture procedures for other candidate nematodes may become available. Nematodes may be most useful against such aquatic pests as mosquitoes, black flies, and certain rice pests. Periodic inoculative releases of nematodes may be necessary for species unable to persist in host populations. In spite of a wide insect host range, there is no convincing evidence that entomogenous nematodes are a hazard to man or other vertebrates. However, many entomogenous nematodes are not host specific and may attack beneficial insects, and pathogens or toxins are associated with some nematodes; thus, careful consideration needs to be given before they are introduced into new areas (197).

A vast number of species of predaceous nematodes have been reported, but relatively few occur in sufficiently large populations in cultivated fields to be efficient natural regulators of nematode pests in annual crops. Most types of predaceous nematodes have low reproductive rates, relative to plant pest species, and their populations appear to be seriously disrupted by soil disturbance. They may be important natural control agents in long-term perennial crops, but only limited investigation of their role has been undertaken. Some predaceous nematodes are omnivorous and can be cultured on fungi to produce large numbers for inoculation studies. However, most predaceous types are not specific in their prey, and prey species are probably taken on the basis of size and random contact alone. Certain predatory species (*Sernura* sp.) are capable of paralyzing much larger prey by injecting salivary secretions, and are known to be predators *in vitro*. Despite the increasingly recognized importance of predaceous nematodes, little practical information on predaceous activity against plant pests is available. Reviews by Boosalis and Mankau (25), Sayre (216), and Webster (257) summarize the state of knowledge on this group.

Several species of nematodes have been reported as damaging aquatic weeds (119, 196, 219, 226) and mycorrhizae of forest trees (206), and one species has been used to control a weed (153).

SNAILS AND OTHER INVERTEBRATES

Two species of snails have been identified as having some potential for weed control. These are the South American snails, *Marisa cornuarietis* and *Pomacea australorbis* (38). The weed control potential of the *Marisa* snail was demonstrated in studies concerning its use as a biological control for the disease bilharzia (193). *Marisa* snails, by consuming aquatic vegetation, also consumed the eggs of the schistosome-bearing snail, *Australorbis glabratus*. Research done in Florida on the *Marisa* snail demonstrated that, under certain circumstances, the snail was capable of providing significant control of submersed aquatic weeds (222). However, being a tropical snail, it failed to overwinter in numbers adequate for continuous weed control even in the Miami, Florida area, and, additionally, it was found to be an indiscriminant feeder (20). The *P. australorbis*

snail has not been studied extensively enough to provide conclusions concerning its weed control potential.

Recent studies have been made of the use of planaria worms for control of mosquitoes and chironomid midges (266).

MICROORGANISMS

Animal Pathogens

The development of insect pathology as a science is relatively recent (234). Although known for over 2,000 years, the use of pathogens to control insects were first proposed during the 19th century. *Bacillus thuringiensis*, a potent pathogen, was discovered in 1911 and produced commercially in France in 1938. *Bacillus popilliae* was widely used for control of the Japanese beetle in the United States as early as 1939 (82). Information dealing with pathogens affecting invertebrates other than insects has been collated by Johnson (135) and Johnson and Chapman (136); that dealing with viral diseases of insects and mites has recently been catalogued by Martignoni and Iwai (170), and various organisms attacking nematodes were recorded by Esser and Sabers (84). The potential and use of some of the better known insect pathogens in pest control are documented in several recent reports and technical publications (1, 85, 185, 186, 264, 265).

Relatively few pathogens have been exploited as pest control agents, and the number of potentially useful pathogens is incompletely known. For example, there are more than 500 isolates of *B. thuringiensis* that are capable of killing a broad spectrum of insect pests species; 350 nuclear polyhedrosis viruses (NPV) and granulosis viruses (GV) have been isolated from insects and mites (170). The investigation of invertebrate viruses is clearly just beginning, and the potentials of pathogens of all kinds for pest control are largely unevaluated.

There are four general kinds of pathogens considered as biological control agents, fungi, bacteria and rickettsia, protozoa, and viruses. The particular biological properties of these different kinds, as well as the state of our

knowledge about them, materially affect the manner in which they are used.

Fungi. The best known of the fungi presently being used for biological control is Beauveria bassiana. Like most fungi, this fungus infects many different kinds of insects. It is widely used in the Soviet Union and the Peoples Republic of China where considerable success is claimed in its effectiveness against forest and orchard pests. In the Soviet Union, the combined use of the fungus with lower doses of insecticides apparently increases the efficacy of the fungus and decreases the amount of insecticide required to effect control. In France, B. tenella has significantly reduced numbers of soil-inhabiting larvae of the European cockchafer. Other fungi presently being studied in the United States include species active in control of the green peach aphid, the spruce budworm, and several lepidopterous pests of soybeans and cotton. In addition, fungi are being studied for use in the control of the citrus rust mite, spider mites, as well as the blueberry bud mite and the citrus bud mite. Several fungal genera, including Coelomomyces, Lagenidium, Entomophthora, and Culicinomyces, show potential as control agents against the aquatic larval stages of mosquitoes and against whiteflies.

Naturally occurring fungal epidemics have materially reduced populations of some pest species, such as the seed corn maggot, by killing the adult flies. In nature, fungal epidemics depend upon rather precise conditions of temperature, humidity, and host density. Thus, to use fungi effectively in biological pest control, it may be necessary to manipulate the critical physical features of the local environment or devise methods of making the fungus more tolerant.

Fungi may act as either parasites or predators in their role as biological agents for nematode control. Parasitic or endozoic fungi which attack nematodes are common in soil, but little is known about their biology. Many species do not interact with nematode pests since the spores must be ingested; therefore, they are of importance only in the population dynamics of free-living nematodes. Fungi with spores which penetrate the nematode cuticle may have some importance as regulators of pest species; but of these only

one species, *Catenaria anguillulae*, has been studied, and currently its status as a biocontrol agent remains controversial. The endozoic Phycomycetes (*Haptoglossa* sp.) with nonmotile spores which penetrate the nematode cuticle, and some of the nematode-parasitic Phycomycetes appear to be important; but the obligate nature of the parasitism of most of them presents great difficulty in culturing them.

In comparison with the literature on other groups of nematode antagonists, the literature on the predaceous (nematode-trapping) fungi is extensive. Many species enmesh or ensnare nematodes by means of constricting and non-constricting mycelial rings or by a variety of organs with adhesive surfaces or coatings. Nematodes are known to be attracted to such trapping organs. Almost all species are facultative saprophytes of varying degrees and are easily cultured. Although they can be produced in large quantities, their ability to rapidly colonize and exploit soil microhabitats is limited (54).

Nematode-trapping fungi are abundant and active in nature, but how abundant and under what conditions they thrive is not clear. Predaceous species of *Arthrobotrys*, *Dactylaria*, and *Monacrosporium* are particularly abundant in both species and numbers in the rhizospheres of long-term perennial crops, and they appear to be important factors in population dynamics of nematode pests in such crops as peach, citrus, and grapes.

The integration of chemical control with the activity of nematode-trapping fungi appears possible. Mankau and Imbriana (167) and Mitsui (181) showed that certain nematode-trapping soil fungi tolerated up to 700 parts per million of ethylene dibromide in culture media, suggesting that nematicides may be metabolized by the fungi. The fungi tolerated direct exposure to dosages considerably higher than nematicidal field rates, suggesting that nematicides do not alter whatever biological control is contributed by predaceous fungi. Results of these investigations and those of Cayrol *et al*. (42) suggest that some fungal enemies of nematodes are not adversely affected by currently used nematicides and are compatible with integrated control.

Production of fungi for use as biological agents involves several considerations, such as loss of virulence when maintained on artificial media and the lack of true conidia,

which are rarely produced in submerged cultures. The technology for use of fungi is not well developed or understood. Fungi are well-known allergens, and this property will need to be critically explored prior to their exploitation for use in pest control.

Bacteria and Rickettsia. The first entomopathogens to be approved for insect control and subsequent commercial production were the spore powders of *Bacillus popilliae*, active against the Japanese beetle grubs, and the formulations of the delta-endotoxin produced by *B. thuringiensis*, which are toxic to the larvae of many kinds of moths and butterflies feeding on many crops and forests. The potential of both agents has not been yet completely exploited. *Bacillus popilliae* is highly effective against the Japanese beetle, and successful development of production by submerged fermentations could greatly broaden the value of this agent. The delta-endotoxin produced by *B. thuringiensis* is widely used on lettuce, cole crops, leafy vegetables, and tobacco. It has recently been shown to be highly effective in the control of lepidopterous pests of stored grains and may replace certain chemical controls in this area. Formulations of the toxin have shown considerable promise for the control of several major forest insect pests, including tent caterpillars and webworms, gypsy moth, tussock moths, and spruce budworm. Moderate improvements in the insecticidal activities of *B. thuringiensis* formulations and application technology are needed to achieve practical and economic control of other forest pests. The toxin is also useful in controlling *Heliothis* on cotton. The HD-1 isolate of *B. thuringiensis* is used commercially in the United States, but other isolates are known to produce toxins that are more effective. In the Soviet Union, at least, four different *B. thuringiensis* formulations are used in insect control programs.

In the United States another *Bacillus* species (*B. sphaericus*) that produces a toxin that kills mosquito larvae is being studied. The bacterium may multiply and persist in the aquatic environment, can be produced in large quantities, and pilot plant-sized quantities have been formulated for various field trials.

Bacteria are also useful for nematode control, although as yet not intensively exploited. Greenhouse tests using *B. penetrans* to control root lesion and root knot nematodes

are very promising (166). In potted soil, the pathogen can destroy a population of root knot nematodes in a few generations of the host. The bacterium appears to be rather host specific. For example, an isolate from California was infective only to four species of root knot and to one species of root lesion nematodes (165). Nematodes not attacked by the California isolate have been reported as hosts elsewhere and it appears likely that there are biotypes of the pathogen.

Bacillus penetrans lends itself to manipulation as a biological control agent because the spore stage of its life cycle is resistant to environmental adversity. The spores fill the nematode body, causing sterility and eventually death. When the nematode disintegrates, the spores are released into the soil where they may remain viable for many years (168). The fact that the somewhat similar "milky spore disease" organisms of insects have been grown *in vitro* lends hope for comparable success with this nematode parasite as a microbial agent to be utilized commercially against nematode pests. No adverse effects in its use are anticipated, but an efficient means of mass-producing it must be found.

The rickettsia are all obligate intracellular parasites of blood-sucking arthropods such as fleas, mites, lice, and ticks. As a rule, the rickettsia do not harm their arthropod host, but are transmitted by the arthropod host to vertebrate animals such as man, where they cause disease. The possibility of manipulating rickettsia genetically to adversely affect their arthropod hosts remains to be explored.

Protozoa. The use of certain protozoa, particularly microsporida, has been proposed for many years; however, few serious attempts have been made to utilize them to suppress insect pests. Several species are currently under investigation. For example, one (*Nosema locustae*) causes a disease of grasshoppers. Small plot test studies have established that distribution of 1 million spores of *N. locustae* per acre will cause a 50 percent reduction of the grasshopper population, often sufficient for effective control. About 30-50 percent of the survivors harbor the protozoan and lay fewer eggs, many of which will not be fertile. Eggs that do hatch produce diseased insects which can carry the pathogen into succeeding generations. In

1976, 16,000 acres of rangeland were treated with _N. locustae_ and compared with conventional insecticide treatments and with other land left untreated as a control. No final conclusions can be drawn until the experiment is completed in 1979.

Another species of _Nosema_ has shown promise in field tests against the spruce budworm. The disease appears to persist into subsequent generations. Another promising microsporidian is a pathogen of mosquitoes of the genus _Anopheles_, vectors of human malaria. Treatment of breeding areas with the protozoan used as a larvacide was not effective at the doses tested, but the infected adult mosquitoes survived such a short time that they were unlikely to transmit malaria.

Viruses. More than 700 species of insects and several species of mites are reported to have viral diseases. David (65) and Loewenberg _et al_. (163) have recorded a viral disease of the southern root knot nematode. Most of those affecting insects are either nuclear polyhedrosis viruses (NPV), or granulosis viruses (GV), both referred to as baculoviruses, or cytoplasmic polyhedrosis viruses (CPV). More than 320 viruses have been isolated from over 250 insect and mite species of agricultural importance, and at least 38 arthropod species have been examined in terms of control with viruses that attack them (85). Production of viruses from five species of insects has been industrialized on a pilot basis in the United States. Of these, the gypsy moth NPV and the Douglas-fir tussock moth NPV are of proven effectiveness as biocontrol agents. NPV's have been widely used for control of the alfalfa caterpillar in California and for control of the cabbage looper; others have been used against cotton pests in Egypt and Africa.

Plant Pathogens and Microbial Antagonists

Microbial organisms are useful both for weed control and for the control of plant pathogens.

Plant Pathogens for Weed Control. Most recent work on the use of plant pathogens to suppress or eliminate weeds centers on the use of fungi. Fungi are attractive as biological control agents because they are ubiquitous, highly host speeific, destructive to the host, persistent, and can be

produced readily in the laboratory (47). Two approaches have been developed to achieve fungal control of weeds. The classical approach employs an initial inoculation of the weed with self-sustaining pathogens which require no further manipulation. The second, or mycoherbicide approach, involves an annual application of endemic or foreign pathogens in a manner similar to the use of herbicides. The classical approach is probably better suited to control aquatic, pasture, or rangeland weeds where annual application of a pathogen for elimination of weeds is not economically feasible. Persistence and efficient natural dispersal of the pathogens, exceptionally well demonstrated by the rust fungi, are the keys to successful suppression of weeds under the classical approach. The mycoherbicide approach is better suited to annual weed control in cultivated crop lands and other areas where rapid elimination of weeds is desirable. Pathogens which can be produced *in vitro* are best suited as mycoherbicides.

The approach used may be dictated by the pathogens available, their specificity, the degree of control required, and economics. Certain pathogens will be eliminated from consideration in some situations by the above criteria. Day (66) has suggested that biological control agents could be most useful to control climax weed species.

Several successful examples of the classical approach to the use of pathogens include two rusts: *Puccinia chondrillina*, which was introduced into Australia in 1971 to control skeletonweed, and *Uromyces rumicis*, which is credited with the suppression of dock in Europe (60, 109, 111, 134). The former has been introduced and the other is being considered for introduction into the United States for control of these weeds. Other pathogens are being considered for introduction into the United States to control waterhyacinth and the milkweed vine infesting citrus.

An example of the mycoherbicide approach is use of an endemic host-specific *Colletotrichum* species to control northern jointvetch in rice (62, 229). Weed infestations have been reduced 95-100 percent by single aerial applications of fungus spores. Another endemic fungus is being evaluated as a mycoherbicide for control of milkweed vine (34). This endemic fungus has achieved a measure of success in killing the vine, particularly seedlings, in field and greehouse tests. Conway (53) has recently shown

that a leafspot fungus (Cercospora rodmanii) is responsible for decline of waterhyacinth when applied as a mycoherbicide in field and greenhouse tests. Other endemic fungi are known or are presently under study (96, 150, 195, 260, 268). A number of foreign weed pathogens are known (1, 46) and may be useful in control of cropland and aquatic weeds. Weed control through interaction of plant pathogens and insects has been demonstrated (46, 77, 78).

Microbial Antagonists. Numerous biological agents exist for control of plant pathogens (12). Disease suppression benefits from these have been realized for many years through bioenvironmental management by use of selected cultural practices. The mechanisms of disease control in these cases are seldom understood, though research has shown that induced resistance, hyperparasitism, and antagonism are the key phenomena involved. While successful examples of application of biological control on a commercial basis have been few, many others show potential.

An interaction between a pathogen and a host, which occurs in the host and makes the host more resistant to a second pathogen, is called induced resistance and is a form of biological control. Many combinations of viral, bacterial, or fungal pathogens provide examples of induced resistance in the host (67, 68, 114, 169, 212, 267). These may be variously called acquired resistance, cross protection, interference, and interactions. There are many mechanisms involved, but these are not well understood. Most examples have been demonstrated under laboratory and greenhouse conditions. Field results are known; for example, Helton (116) inoculated trees with Prunus ringspot virus which induced resistance to Cytosporella cankers. Tomato seedling transplants in the Netherlands are protected from severe tobacco mosaic virus infection by resistance induced by prior inoculation with an avirulent form of the virus (200).

The parasitism of one parasite by another is termed hyperparasitism and appears to be a common phenomenon in nature. Its significance under field conditions is difficult to assess, and methodology for exploitation as a biological control measure has not been developed. Hyperparasitism may occur between two fungi (mycoparasitism), a bacterium and a fungus, two bacteria, a virus and bacterium, or a virus and fungus. Mycoparasites initiate parasitism either

by direct penetration to the host cell or by first coiling around the host hyphae and penetrating by infection pegs (25). Host structures other than mycelia, such as reproductive structures, may be attacked. Mycoparasites of the shoestring fungus (21), a number of phycomycetes (37), Rhizoctonia (23), and others are known (16, 75, 140, 224). Many other instances of destructive mycoparasitism have been reported.

Less attention has been given to bacterial parasitism of fugal pathogens; but exolysis, or partial digestion of cell walls by bacteria, may be an important common form of parasitism (12). Mitchell and Alexander (179) attributed the control of the banana wilt fungus to digestion of the chitinous cell walls of the pathogen by soil bacteria.

A small, comma-shaped bacterium (Bdellovibrio bacteriovorus) is parasitic on other gram-negative bacteria. An isolate from the rhizosphere of soybean roots was used to inhibit development of another pathogen on soybeans when the two were inoculated simultaneously (217).

The phage-bacterium relationship may be a useful biocontrol mechanism. The phage penetrates the bacterial wall and multiplies within the protoplast, subsequently rupturing the wall. Though it is common knowledge that phages reduce numbers of bacteria, they have not been exploited for biological control. The destructive capabilities of a virus on a fungus have been well documented by serious losses in the commercial mushroom industry because of virus diseases. Viruses have been reported in a number of pathogenic and saprophytic fungi (121), but their utilization for control of plant pathogens is yet to be undertaken.

Antagonists may serve as biocontrol agents by their competition for substrate or by their attempts to occupy an ecological niche and thereby interfere with pathogenicity. Organisms can also be antagonistic to each other by producing metabolic products or antibiotics. Both of these types of interaction have been used in the biocontrol of plant pathogens (61, 117, 225). Application of antagonists to seed is effective against both seed and soilborne pathogens (30). Damping-off was prevented or reduced in pine (154), corn seedlings (44), and in tomato seedlings (180) after seeds were coated with antagonistic bacteria.

Some of these bacteria were shown to be antibiotic in culture to the several damping-off or seedling blight pathogens.

Protection from seedling blight was obtained by coating beet seeds with common saprophytic fungi (162); and oat seedlings (247) and corn seedlings (44) were protected by coating seeds with another common soil-inhabiting fungus. Protection against seedborne pathogens was obtained also by application of antagonists such as *Trichoderma* and *Penicillium* species to seed (176).

While these and most other such studies were done in the greenhouse, the application of the common hay bacillus *Bacillus subtilis* and a fungus *Chaetomium globosum* to corn kernels before planting in the field resulted in less seedling blight, less root disease, better stands, and higher yields than in corn from untreated kernels (152). Recent unpublished work from Minnesota indicates improvement in stand and yield of soybeans in the field by application of bacteria in peat to soybean seed, even where pathogens were present. Stands of sweet corn in the field were also improved by application of several different bacteria to kernels before planting.

Crown gall (*Agrobacterium tumefaciens*) of peaches has been successfully controlled by seed and root inoculation with certain related nonvirulent bacterial strains (*radiobacter*) (125, 139). The organisms applied to seeds were those originally isolated from seed on root surfaces and soil; this enhances their chances of becoming established and being effective antagonists at the seed or root surface at planting or shortly thereafter. There is evidence that this successful use is through the mechanism of bacteriocin production (252). Bacteriocins are specialized antibiotics. They are nonreplicating, bactericidal protein-containing substances produced by certain strains of bacteria with specificity primarily against related bacteria. The use of bacteriocin-producing strains of bacteria to kill sensitive strains of the same or closely related species is in initial stages of experimentation. The costs of such control will probably be less than other types of control tested to date.

Evidence suggests that application of organisms to seed, either with or without coating materials, is feasible on a commercial scale and has the advantage of not requiring a

treatment procedure by the grower. Such treatments could apply also to cuttings or other propagative plant parts. Results compare favorably with chemical seed treatments currently used in which the technology of application is similar. There is evidence also that organisms applied to seed give protection for a longer period of time than chemicals applied to seed, as organisms may multiply and maintain their inoculum potential at the seed and root surfaces. This dominance of antagonists at the seed and root surfaces may be attributed to a greater competitive saprophytic ability or to the production of antibiotic substances that deter root pathogens.

Interactions of microorganisms on foliage or in the phyllosphere can result in disease control. The phyllosphere is a continuum of living and nonliving entities in a microclimate surrounding foliage. Microorganisms in the phyllosphere include epiphytic residents and casuals (159), and it is here that endophytes (232) and pathogens begin parasitism. Interactions between saprophytic and pathogenic organisms in the phyllosphere involve several mechanisms that reduce disease incidence and, when understood and properly utilized, will provide a desirable addition to the methods for plant disease control.

Although few examples of antagonistic interactions between saprophytic and pathogenic bacteria in the phyllosphere exist, they offer a stimulus for additional research (58). Recently, Leben (160) was successful in reducing bacterial seedling blight of soybean. This was accomplished by applying antaonistic bacteria to seed where they subsequently became a major resident of the phyllosphere. This example, like most others, was developed in the laboratory and greenhouse; field tests are in progress.

Another interaction in the phyllosphere results when saprophytes or nonpathogenic isolates of pathogens are applied as protective agents for the control of fungal pathogens. Diseases caused by _Alternaria_ on three different hosts were reduced when protective fungi were applied to foliage up to 3 days prior to inoculation wih the pathogen (93, 231, 251). Disease control up to 80 percent was achieved. Disease control in the phyllosphere does not appear to involve any direct response of the host plant, but involves high numbers of saprophytic organisms.

The future success of biological disease control in the phyllosphere seems to depend upon the selection of appropriate protective microorganisms and applying these to plants at a critical time under conditions which favor the antagonists. Both an increase in control effectiveness and development of economically feasible controls for field conditions are long range goals. The possibility appears remote that application of saprophytic organisms to plants might lead to undesirable features.

An interesting but poorly understood technique of biological control involves a principle that has been termed exclusive hypovirulence (102). Spontaneous healing of chestnut blight cankers on European chestnut was observed in several locations in Europe. Cultures of the blight fungus recovered from healing cankers were almost completely nonvirulent (hypovirulent). The ratio of these hypovirulent strains to virulent strains isolated was directly related to the health of the chestnut grove. Subsequent studies showed that active cankers could be cured by inoculation with the hypovirulent strain, and that 3 years after introducing the hypovirulent strain in a chestnut grove, it became dominant and the disease regressed.

Cultures of a French hypovirulent strain were used in the United States to inoculate cankers on American chestnut and were effective in controlling cankers on trees inoculated with a French virulent strain, but were less effective against an American virulent strain (2). Van Alfen et al. (249) transferred hypovirulence into American strains of the blight fungus and demonstrated that hypovirulence was caused by a cytoplasmic determinant that is transferred by hyphal anastomosis.

If the technique of exclusive hypovirulence succeeds in the case of the chestnut blight, it may offer a significant new disease control method, providing hypovirulent strains of other pathogens can be found.

Biological control measures for diseases of forest trees and woody plants that are currently being utilized or proposed generally involve the same principle -- the topical application of competing or antagonistic microorganisms to the surfaces of freshly made wounds through which certain disease- or decay-causing fungi enter. One successful

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biological control of a forest tree disease on a commercial scale is the use of the fungus Phlebia (Peniophora) gigantea to control Fomes annosus.

Rishbeth (207, 208) in England was the first to suggest the use of P. gigantea as a possible alternative to chemicals for stump protection, and showed that stump inoculation with a conidial suspension prevented stump infection by F. annosus. Since 1962, stump treatment has been a routine practice in plantations managed by the British Forestry Commission and inoculum is produced commercially (209). Phlebia gigantea also proved effective in the United States, and Hodges (120) showed this treatment compares favorably in cost with chemical controls.

Several workers have reported success in preventing infection by disease and decay fungi through pruning and other wounds on the trunks of trees. Carter (40) was able to prevent infection of apricot by inoculation of the pruning wounds in apricot with spore suspensions of Fusarium lateritium. Later, Carter and Price (41) applied benomyl for immediate protection and a benomyl-tolerant strain of F. lateritium for long-term disease control. Grosclaude and Dubos (103) prevented Stereum purpureum infection of plum trees in France by treating pruning wounds with conidia of Trichoderma viride. They used modified standard pruning shears for application of the spores to the cut surface as the branches were pruned. Pottle and Shigo (198) prevented invasion of wounds on trunks of red maple trees by decay fungi by applying spore suspensions. The exact mechanisms involved in these successful treatments are not known, although a likely explanation is competition for the substrate between the pathogen and control organisms.

Direct biological control of a soil-borne plant pathogen by a single antagonistic fungus or bacterium can be easily demonstrated in sterilized soil free of other microbial competition. However, the direct application of control agents to field soil generally has met with little success until recently. Following a report by Wells et al. (258) of biological control of Sclerotium rolfsii by Trichoderma harzianum in field experiments with tomatoes, peanuts, and lupines, Backman and Rodriguez-Kabana (11) developed a system for growth and delivery of T. harzianum for field soil. The antagonist was produced in quantity on

diatomaceous earth granules impregnated with a molasses solution plus potassium nitrate and potassium dehydrogen phosphate. The granules with T. harzianum were then mixed equally with other sterile, dry molasses-impregnated granules and distributed over-the-row to peanuts 70 and 100 days after planting. Results showed that the treatment significantly reduced pathogen incidence and damage as much as that gained by fungicide treatments; yields were also increased. The mechanism of action is thought to involve, besides antibiosis, a pH-induced competitive advantage for proteolytic enzyme production by T. harzianum which inhibits S. rolfsii (211).

This biocontrol system has important advantages: (1) blackstrap molasses used as a nutrient for the antagonist in the granules is inexpensive; (2) granules are lightweight and deliverable with standard machinery; (3) field results are reproducible; (4) and because T. harzianum is a common soil-inhabiting saprophyte, it should pose no serious environmental hazards. This method could serve as a model for delivery of other antagonists to field crops.

Biological control of certain root diseases, such as those caused by Pythium and Phytophthora, is often attributed to the presence of mycorrhizae (171). While plants growing in their native habitats are naturally infected with the appropriate mycorrhizal fungi, those introduced into new areas or into modified habitats such as disturbed surface areas often need to be inoculated before they are planted in the field (172). With relocated plants grown in nurseries, the opportunity exists to inoculate with both ectomycorrhizal (171) or endomycorrhizal (15) fungi, which would result not only in increased efficiency in relation to plant growth but also in protection against soil-borne pathogens. Methods for nursery inoculation of pine seedlings with mycorrhizal fungi have already been developed (172) and might be used for other fungi.

HIGHER PLANTS AS COMPETITORS AND ANTAGONISTS

Higher plants may function as biological control agents for other plants through a specialized type of interspecies competition involving the production, by some plants, of physiological chemicals that inhibit the growth of other

plants. This phenomenon, called allelopathy, is well established among land plants, animals, and microorganisms. It can be assumed that allelopathy is a phenomenon also active among aquatic plants (95, 122). Higher plants may also be antagonistic toward plant parasitic nematodes, and some are believed to be antagonistic toward some insects (238).

Species of spikerush influence neighboring vegetation, which makes it possible for these diminutive plants to compete successfully with much larger species (192). Allelopathy is the probable basis for the successful competition. Research is in progress to further characterize the allelopathic relationship, and to extract, isolate, and identify the chemical produced by spikerush. Other research is being carried on to develop practical methods by which spikerush may be used as a biological control for the larger and more troublesome species of aquatic weeds.

Allelopathic relationships are known to exist between certain agricultural crops, between weeds and crops, and between various species of weeds and other noncrop plants (122, 220). Although allelopathy has been largely neglected as a useful tool in biological control of weeds, it may lead to an entirely new weed control technology.

Many plants have been tested for antagonistic properties against plant parasitic nematodes. Much of this research has been conducted or reviewed by Brodie *et al*. (27, 28, 29), Suatmadjii (239), and Webster (257). While several plants possess antagonistic properties, crotalaria, marigold, and pangolagrass are especially effective.

Crotalaria and marigold control several of the major plant-parasitic nematodes that cause extensive losses in crop plants. Pangolagrass appears to be more restricted in scope and is effective primarily against the root knot nematode (*Meloidogyne sp*.) (262), but Ayala *et al*. (10) reported that it controlled several other plant pathogenic nematodes as well. These plants suppress nematode populations beyond the suppression obtained by fallow, nonhost crops, or nematicides. In some cases effective control lasts more than one season (177, 178).

Marigold has been used on a field scale in the Netherlands, Ceylon, Rhodesia, and India to control root lesion and root knot nematodes on tea, tobacco, and potato

(63, 189, 194, 254). Crotolaria has been used to control root knot nematodes in tomato transplant production by growing it after transplants are harvested and then plowing under before flowering. Pangolagrass has not yet been used commercially.

Although at least two of these plants have been used on a limited basis, none has had widespread acceptance. The reasons for limited acceptance and use are that crotolaria and marigold have no commercial value other than as green manure crops, crotalaria seeds are poisonous to livestock, marigold is difficult to establish in the field, marigold and crotalaria usually must be grown during the same season and instead of the crop to be protected, and pangolagrass must be grown for 12-18 months to be effective.

The future use of plants currently known to be antagonistic to nematodes will likely be limited to special circumstances. For example, marigold may be used by the home gardener who may value the ornamental aspects of the flower as well as the nematicidal benefits. Marigold may also be useful in subtropical and tropical climates where it could be grown for 3 to 4 months after the main crop has been harvested and before the next main crop is to be planted.

V. RESOURCE REQUIREMENTS AND DEVELOPMENTAL CONSIDERATIONS

The feasibility of using biological agents for pest control will depend upon the resources required and the technology available for utilization. These factors include the availability of biocontrol agents, knowledge of their biology and interactions with target pest species, existence of support facilities and technology, the anticipated benefits, costs, and environmental and health risks. The efficient implementation of a management or biocontrol operation is also dependent on thorough consideration of these factors.

The selection of suitable biological agents may be simple or complex, depending upon the state of knowledge of agents to be used and the intricacies of their relationship with the environment and the target pest. Microorganisms of potential value as antagonists of plant pathogens may be present and active but may not be readily apparent to the observer. Baker and Cook (12) provided useful suggestions for seeking antagonistic microorganisms, along with the observation that antagonists are where you find them, but some areas afford better hunting than others.

Predators, parasites, and pathogens that attack invertebrate pests, and organisms useful for weed control, are customarily sought in association with the pest or related species (17). It is generally understood that selection of entomophagous insects from a wide range of source populations will increase the genetic diversity of the culture stock and thus improve the chances for successful control of the target pest throughout its range. It is also important to make use of whatever information is available about the capacity of organisms to adjust and adapt to their natural environment (174). The following discussion concerns information necessary to assess the feasibility of pest control by the use of biological agents.

SYSTEMATICS

The first step in gaining knowledge of pest species and their possible biocontrol agents is accurate identification. Accumulated knowledge about the organisms can usually be retrieved and put to use, even though our present methods of information storage and retrieval may be cumbersome and

inefficient. Even tentative identications that serve to associate unknown forms with related known kinds about which biological knowledge is available provide bases for helpful deductions. The contributions of taxonomy and systematics to biological control go far beyond providing identifications, as has been pointed out by Clausen (49), DeBach (69), Sabrosky, (214), and Schlinger and Doutt (218). The ability of scientists to provide accurate identifications presupposes a comprehensive knowledge of the world's fauna and flora, an objective still far from realized because of the number and variety of life forms and the diversity of developmental stages.

INFORMATION STORAGE AND RETRIEVAL

Effective use of accumulated information concerning biotic agents for pest control requires that it be readily available. The need to find better ways to handle the rapidly growing mass of biological and related information has been widely recognized. Of the numerous systems proposed (26, 79, 94, 138) all fall short of meeting the specialized needs of broadly based pest control programs. Because the use of biological agents needs to be coordinated with other pest management strategies, and involves knowledge of biota from many parts of the world, the information storage and retrieval system that services such activities must be essentially global in scope. The desirability of applying computer technology to this task is understood; what is required is concerted action that will result in a truly comprehensive information system for biology and ancillary disciplines that impinge upon pest control activities. Following are examples of the important information categories needed:

1) Biological literature. This category is reasonably well covered by such programs as BioSciences Information Service (BIOSIS) of Biological Abstracts. Continued improvement of this type of coverage, coordinated with information in other categories, is desirable.

2) Host and biotic agent records. Development and maintenance of a cross-indexed system of hosts and biological agents is essential. Ancillary information on occurrence records and normal geographic range contained in unpublished and published records should be incorporated in such a computerized system. An alternative arrangement would be development of a taxonomically-based, computerized

system of sufficient scope to contain the desired information about pests and their natural enemies. The data file should include a list of current sources from which biotic agents can be obtained and the data file should be kept current if it is to be useful.

3) Introduction and establishment records. Accurate information is not readily available about successes, partial successes, and failures, that is, a complete record of biocontrol agents that have been permanently established in various geographic areas. Laing and Hamai (156) summarized successful uses of all types of biocontrol agents for control of insects and weeds on a worldwide basis, and DeBach (71) provided a similar summary for entomophagous insects. A reasonably complete record of introduction of biocontrol agents for the control of insect pests and weeds in Canada is available (55, 175). Clausen (50) prepared an account of biological control efforts against insects in the continental United States that is believed to be reasonably complete up to 1950 insofar as the record of importations and establishment is concerned. A more comprehensive summarization of work in the world, covering activities against insects and weeds is in press (52). Improvement or extension in subject matter scope and geographic or temporal coverage of this type of information would be of inestimable value. Efforts to assemble and organize information of this sort dealing with other types of biocontrol agents used against pests is also essential. Documentation of planned introductions should be by preservation of voucher specimens whenever appropriate and feasible (210).

IMPORTATION AND QUARANTINE

The discovery of potentially useful biocontrol agents often involves overseas exploration. These activities are currently accomplished through various Federal and State agencies in this country and by agencies of several other countries. When the target pest is of foreign or domestic origin, movement of the biocontrol agents from one part of the world to another is frequently necessary. If there is adequate time, and suitable facilities are available, the agents may be thoroughly studied before being shipped from one region to another; if not, the agents are often collected and shipped without critical study. Organisms imported from foreign countries to the United States are usually held under quarantine for at least one generation

to permit detection and removal of contaminating organisms such as secondary parasites, plant pathogens, and hazardous or unwanted host materials. There may be opportunities during the quarantine period to confirm essential aspects of the biology of the agents, and to gain additional information of potential use in biocontrol. Also, it may be desirable to increase the numbers of the agent as a means of enhancing the possibilities for successful establishment. Quarantine facilities are essential to the safe and successful conduct of biological control activities. A comprehensive discussion of quarantine rationale, procedures, and facilities is available (88, 90).

There are, at present, 10 quarantine facilities in operation in the United States that are authorized to handle biological control agents:

Beneficial Insects Quarantine Laboratory,
Virginia Polytechnic Institute and State University
Blacksburg.

Beneficial Insect Research Laboratory,
ARS, USDA, Newark, Delaware.

Biological Control Laboratory, Division of Plant Industry
Florida Department of Agriculture and Consumer Service, Gainesville.

Biological Control of Insects Research Laboratory,
ARS, USDA, Columbia, Missouri.

Biological Control of Weeds Laboratory,
ARS, USDA, Albany, California.

Plant Disease Research Laboratory,
ARS, USDA, Frederick, Maryland.

Quarantine Laboratory, Division of Biological Control,
University of California, Albany.

Quarantine Laboratory,
Hawaii Department of Agriculture, Honolulu.

Quarantine of Insects Research Laboratory,
ARS, USDA, Stoneville, Mississippi.

Quarantine Laboratory, Division of Biological Control,
University of California, Riverside.

These facilities have been certified by the Animal and Plant Health Inspection Service, U.S. Department of Agriculture, as required by current policy, as to adequacy for the purpose of handling potential pest organisms. None of these laboratories is adequate to handle all kinds of biocontrol agents, nor is any intended to do so, because procedures and facility design requirements differ for the different types of organisms to be processed through quarantine. Orderly development of quarantine facilities will depend upon the direction and degree of expansion in biological control programs. Factors that must be considered include the development and adoption of guidelines for the construction and operation of facilities, as well as provision for periodic inspection of facilities and operational procedures to assure continued adequacy of of the facility and adherence to approved procedures.

BIOLOGICAL AGENT RESOURCE CENTERS

The practical use of biological control agents requires that the appropriate species be available in adequate numbers to accomplish a particular objective. Because most agents are highly specific for the developmental stage of the pest they attack, cultures of a considerable variety of biological agents may be used against a single pest. Some agents, such as viruses and many plant pathogens, may be held for long periods of time in dormant states; others, such as most insect and nematode species, can be held for only relatively short periods of time without being propagated. Agents of this sort are customarily maintained in cultures or retrieved from "wild" populations as needed (87). Most subcultures of biocontrol agents are available only from research laboratories or quarantine facilities. However, the desired kinds and numbers of agents needed for biological control programs cannot be routinely provided from such sources without seriously impairing their primary missions. The logical solution to the problem appears to be the development and operation of biological agent resource centers--installations developed and maintained for the specific purpose of obtaining and providing subcultures and populations of a broad array of biocontrol agents.

There are presently no installations capable of meeting the demands for the kinds of agents needed for a comprehensive biological control program, although there are numerous private installations and several national or international centers that acquire, maintain, and preserve stocks of biological agents. A list of insect pathogens (bacteria, fungi, protozoa, nematodes, rickettsiae, and viruses) available for distribution in 1970, and the sources from which they could be obtained, are given in Burges and Hussey (32: appendices 5 and 6). However, the installations maintaining such cultures, like those that maintain stocks of other kinds of biological agents, serve a multiplicity of technical and scientific interests and are not specifically designed to provide supplies of biological agents. Neither are the numerous research facilities that exist at the State Agricultural Experiment Stations, Federal and State laboratories, and universities.

Although collectively, and over a considerable period of time, these centers and laboratories maintain a great variety of material of potential value, the kinds and quantities of agents available at any given time are usually limited. From the standpoint of serving the needs of broadly based biological control programs, coordination of effort among the many installations engaged in this activity is essential. Information as to sources and agents available is currently difficult to obtain. To some extent such information becomes known through informal cooperation and communication among research scientists. An effort is being made by the International Organization for Biological Control (IOBC) and the Commonwealth Institute for Biological Control (CIBC) to formalize and coordinate the exchange of information of this nature. Information regarding insects useful in pest control is being accumulated by the Insect Identification and Beneficial Insect Introduction Institute of the U.S. Department of Agriculture. Information and culture exchanges in the specialized fields of weed science, plant pathology, and nematology are primarily informal and dependent upon personal communication among interested parties.

The improved efficiency needed to realize the full potential of biological agents for suppression of pest populations will require improved technologies and better coordination of efforts to collect, preserve, maintain, and propagate populations or cultures of useful agents.

Assuming that the source material available is reasonably representative of the desired agents that occur in nature, particular care must be exercised to maintain the original qualities of the stock during the propagation processes, or at least minimize reduction of genetic diversity and loss of desirable traits. The intended use of laboratory-produced populations or cultures may have some bearing upon what features are most important, but, in general, retention of those components of the biology and behavior of a species essential to its survival in nature is considered highly desirable. This aspect of biological agent propagation is particularly critical for those organisms that must function efficiently in the field in finding hosts or mates, as is required of entomophagous insects or those used in the sterility method of pest control (35, 43, 123, 164). The intentional production of stocks with inferior characteristics, to be used to reduce the reproductive potential of noxious forms by altering or replacing hereditary material, is an exception to the above generalization. In the case of pathogens of invertebrates, production problems involve standardization of the product, both in terms of concentration and viability. If *in vitro* production methods are used, the presence of contaminants similar in appearance to the pathogen may complicate the standardization process. Individual specific antagonists of plant pathogens may be propagated as in the commercial production of antibiotics.

Monitoring the quality of biological agents propagated *en masse* is an essential step in determination of feasibility. This process involves measuring the interaction of two complex and individually variable entities, the target pest and the biological agent, and inevitably calls for procedures capable of contending with variation (33, 126). Bioassays may often be the only definitive tests.

The extent to which biological agents of various sorts will become available through private enterprise is currently uncertain. The pattern of research and development that has thus far prevailed suggests that, in general, feasibility of production and use will need to be established with the support of public funds before private sector participation becomes significantly large. To date, commercial production of biological agents has been limited to a few pathogens (for example, *Bacillus thuringiensis*, *B. popilliae*, and *Heliothis* NPV) and a few entomophagous insects (for example, *Chrysopa carnea*, *Trichogramma* spp., *Cryptolaemus montrouzieri*, and *Aphytis melinus*). The

pathogens are produced and marketed in much the same way as pesticides, and the feasibility of use is well established. The production and use of entomophagous insects is usually more complicated because of their specialized biological requirements and behavior. Although a few of thesy agents are routinely sold to growers with instructions regarding their use, the more usual arrangement is for the producing organization to use them in pest management programs under contract. The feasibility of pest control by the use of sterile or otherwise genetically altered insects has been investigated largely by publicly supported institutions or agencies. Until profit incentives arise, that pattern is likely to persist.

FACILITIES FOR MASS PRODUCTION OF BIOCONTROL AGENTS

Not all demands for biological agents can be met by resource centers. Only relatively limited numbers or quantities of an agent may be needed for inoculative or establishment releases, but programs designed to eradicate or drastically reduce a pest population within a short period of time, or keep the population within a circumscribed area at low level over extended periods, almost always require massive numbers. The use of pathogens in essentially the same way that pesticides are used, the use of genetically altered insects against populations of the same species, and the augmentation of populations of entomophagous organisms are programs that require large numbers or quantities of the agents on a continuing basis. Releases are usually on a scheduled basis and over large areas, as in the screwworm suppression program in the Southwestern United States and Mexico. The extent to which biological agents can be used as practical alternatives or supplements to other pest management tactics will depend in large measure upon the development of efficient methods of mass producing, handling, distributing, and releasing organisms having the potential for suppression of pest populations. Unlike chemical compounds that can be manufactured, formulated, and stored for subsequent use, most biological agents must be mass produced as needed and released as living organisms at an appropriate time in relation to the development of populations of their pest hosts. Further, most agents useful against a particular pest will have distinctive developmental cycles, behavior, and environmental requirements. The different kinds of agents of potential value to programs of this

sort--microbial pathogens and antagonists, nematodes, mites and insects--require quite different kinds of culture techniques. Thus, it is readily apparent that several different kinds of production facilities are needed.

Mass production facilities should be dependable sources of high-quality biological agents in whatever quantities the pest control program demands. Quality control of the products is a constant requirement (22, 43, 59, 123, 126). During the past two decades the experiences of scientists concerned with culturing and mass production of insects make it abundantly clear that the transition from culturing a few thousands in the laboratory to producing millions of specimens on a scheduled basis entails close coordination of scientific and engineering technology, as well as careful consideration of the economics of the operation (204, 227). Mass production of entomophagous insects has been almost entirely a byproduct of research programs. Most facilities currently engaged in the production of insects for pest control were never intended for mass production purposes but have evolved from research installations through increase in size or other modifications (for example, tropical fruit fly facilities in Hawaii and Mexico, and the boll weevil facility at Mississippi State University). Only a few facilities have been designed and constructed for the express purpose of producing massive numbers of insects for programs of this nature, for example, the screwworm fly production plant at Mission, Texas, and the pink bollworm facility at Phoenix, Arizona. These two installations produce insects for use in sterile insect release programs.

The extent to which mass production of viruses and microbial pathogens and antagonists may be needed is as yet unclear. Production of pathogens in artificial media was discussed by Dulmage and Rhodes (81), and the propagation of arthropod pathogens in living systems by Ignoffo and Hink (133). Production of pathogens in host animals is necessarily a more complicated procedure because production of the hosts entails additional work and expense. However, few pathogens have as yet been successfully propagated for biological control programs in artificial media. Viruses may often be obtained more economically and in greater quantities by collecting diseased hosts during epizootics than by propagation under laboratory conditions, although that practice has associated problems (240). Mass

production of microorganisms antagonistic to plant pathogens is already technically feasible (12).

EVALUATION OF BIOLOGICAL AGENTS

Prior to the implementation of pest control programs a critical appraisal of the practicality of using the agent is essential. This is particularly true if investment of large amounts of energy and resources for mass production of biotic agents is anticipated, but it is no less important to all control programs that involve the use of living organisms. Appraisal of "classical" biological control programs usually begins with determination of success of establishment of the agent, followed by attempts to measure the impact on target pest populations over a period of years. Statistically reliable evidence of the effectiveness of agents used in programs of this type has seldom been available because of the difficulties in differentiating the effects of the agents from the many other population suppression forces that may be operative. The nature of the problem and methods that may be useful in appraising effectiveness of biological control programs are discussed in considerable detail by DeBach and Bartlett (73), DeBach and Huffaker (74) and summarized by Stehr (233).

Evaluation of the effects of biocontrol agents applied or released on a programmed schedule can be made more reliable if dosages or release rates are known and levels and trends of the pest population can be monitored with reasonable accuracy. Evaluation of programs of this type can best be made through large-scale field trials, preferably conducted against geographically isolated pest populations. It is also desirable that the field trials be designed so that the biocontrol agents can be used in combination with other pest management tactics, either concurrently or sequentially, to approximate as nearly as possible actual field situations. Such field trials require massive supplies of the test agents and thus provide opportunities for production processes to be tested and improved. The trials will also provide the needed experience in handling, shipping, and releasing biotic agents of various kinds, activities that nearly always pose unexpected problems. Ideally, large-scale field trials will also provide a basis for estimating cost/benefit ratios of pest control programs that are to be implemented. They are a necessary prerequisite for the

intelligent planning of research priorities and the identification of potentially effective biocontrol agents.

ENVIRONMENTAL CONSIDERATIONS

In contemplating the environmental changes that may result from the use of biocontrol agents for pest control, it is necessary to consider that the environment into which the agents will be introduced already includes a vast interacting network of organisms, of which the target pest is a part. Environmental factors are interrelated and dynamic; the pest/biocontrol agent interaction cannot be disassociated from the many other interactions that are constantly taking place in the ecosystem they occupy. Among the environmental factors that need to be carefully considered are those that hinder establishment of introduced beneficial organisms. Both abiotic and biotic factors may be involved in what can be termed environmental resistance to invasion. This phenomonon is exemplified in the discussion of biotic interference with insects imported for weed control (99).

The intent of a biological control operation is to mitigate the deleterious effects of pest organisms with the least unfavorable modification of the total environment. Success or failure in the venture depends upon a suitable ecological niche being available for the agent at the time it is introduced. If a suitable niche is not available, establishment of the agent will likely fail, although benefits of a transient nature may result from the releases. Environmental effects on biotic agents may be direct (for example, temperature or moisture stress) or indirect (for example, conditions that increase the ability of hosts to resist, tolerate, or avoid the agent). Most cultural practices, such as tillage, irrigation, and time of planting, and perhaps most of all the use of pesticides, will affect biological agent performance. The complex interactions that take place in ecosystems as organisms respond to the limitations imposed by the biotic and abiotic factors of the environment are discussed by van den Bosch and Telford (250), Hasan and Jenkins (110), and Baker and Cook (12).

The relative importance of a given environmental factor may vary considerably depending upon the kinds of biocontrol agents used and the manner in which they are employed for

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pest control. Those agents that are expected to become permanent members of the pest's ecosystem, as is the case in classical biological control, often require, in addition to their primary host and climatic conditions within their range of tolerance, suitable alternate hosts to assure their survival during periods when the primary host is scarce or absent. There may also be other needs, particularly for entomophagous arthropods, such as secondary food sources for the adult stages and suitable harborage. Except for alternate hosts, essentially the same conditions are required for biotic agents released to augment existing populations of the same species, even though the presumption is that population levels of the agent will decline as host populations diminish. Genetically altered arthropods released to depress resident populations of the same species must survive only until matings with members of the "wild" population have been consumated. Since such agents are subjected to the same environmental stresses as the wild population, appropriate attention to the fitness of the individuals released is important.

An understanding of environmental conditions is particularly important in connection with biological control of plant pathogens, since environment controls the outcome of host-pathogen-antagonists interactions (12). Humidity, dew, rainfall, air and soil temperatures, and soil moisture are all important factors in the interactions between pathogens and control agents at the infection site, the rate at which disease develops, sporulation of the pathogen, and the persistence of the pathogen in the environment. The quantity and quality of soil microbial populations will influence the competitive advantage required for the establishment of introduced antagonists such as Trichoderma, used to control root diseases. A guiding principle in biological control of plant pathogens is to manipulate the interactions so that the antagonist can attack or influence the pathogen at a weak point, preferably the most vulnerable, when the physical environment is favorable to the antagonist, unfavorable to the pathogen, or both (12).

Although insect pathogens are presumably widely prevalent in nature, stable populations do not persist or spread well in the environment. Thus, usually microbial insect control involves several applications of a pathogen to a limited area throughout a season, much as pesticides may be applied. Inasmuch as insect pathogens are also greatly affected by environmental factors, such factors will materially influence

the time and conditions under which the pathogens are applied, although one of the principal problems is applying them in such a manner that they will be ingested by the target pest. Sunlight and other physical features of the environment may rapidly inactivate viruses that are useful for suppression of insect population outbreaks.

SAFETY

Questions of possible adverse consequences of using biological agents for pest control relate largely to their host specificity. Almost absolute specificity is required in the case of phytophagous insects or plant pathogens used for control of weed species so that they will not damage desirable plants. Some insect pathogens or parasites may attack a rather broad spectrum of hosts; possible adverse effects could result if populations of a desirable species (for example, one used for weed control) were inadvertently suppressed. Some sterile insects released *en masse* against smaller resident populations of the same species (for example, house flies and female mosquitoes) could be pestiferous or damage crops, as is done by the adult boll weevils in their feeding or other activities.

The usefulness and environmental safety of biocontrol agents depends upon how they interact with other organisms. It is critical that they be evaluated on that basis. High priority should be given to research on the roles environmental factors have in the establishment, efficacy, and safety of biocontrol agents. Clarification of these roles will expedite and facilitate the development of practices that will ameliorate environmental limitations to their use. Particular attention should be directed to the factors that determine specificity in agent/host relationships.

Safe and safety are relative terms. In the context of this discussion, safe means not harmful to humans or other nontarget organisms; however, what may be safe at one time and place may not be safe under other circumstances. Inasmuch as biotic agents originate in nature and are adapted to niches in particular ecosystems, there should be few hazards when they are used within the environmental framework in which they evolved. Tests of biocontrol agents have revealed no deleterious effects when the agents are used as recommended. Nevertheless, because the

possibilities of long-range effects have not been eliminated, constant vigilance is warranted.

There is an urgent need to develop criteria for safety evaluation of biotic agents to expedite utilization of technologies for their use. Different criteria must be used for different kinds of agents and the hosts involved. Such criteria for safety evaluation should be developed only after appropriate consideration by, and consultation with, scientists knowledgeable about the particular agents. Because the biological potentials of viruses and microbials are the least understood of all the biotic agents used for pest control, particular attention has been directed toward safety considerations in their handling and use. The report of a recent working symposium (240), convened jointly by the U.S. Environmental Protection Agency (EPA) and the U.S. Department of Agriculture to scrutinize questions relating to the safety of baculoviruses, exemplifies the in-depth appraisal needed to assure maximum safety in the use of biotic agents. Recommendations that emerged from the symposium include: Identification of the agent under consideration, testing for efficacy against selected target organisms, specificity testing on both target and nontarget organisms selected so as to be appropriate for individual agents, and periodic review and evaluation of safety data. The findings of the symposium participants support and are in accord with recommendations contained in a recent report by a committee of the U.S. National Academy of Science (186: vol. 1) for revision of registration protocols so as to substitute tests appropriate for the properties of living pathogens. When baculoviruses are supplemented in nature by artificial means, additional public health considerations may arise during production and application. Other safety measures may also be desirable for agents brought into new areas under quarantine.

Because of their presumed greater value as pest control agents, safety considerations for animal pathogens have been concerned primarily with the NPV baculoviruses. The CPV viruses have a wider range of hosts than do the NPV's. This suggestion of a lack of host specificity in the CPV viruses, their tendency to act slowly on their host, uncertainty as to details of the host-infection processes, the general absence of information about their effects on nontarget animals, and perhaps other considerations, have resulted in only negligible research on their use.

No entomogenous fungus useful for insect control has been found to be capable of infecting living plant tissue. Guidelines have been developed for testing hazards to humans and other vertebrates. Because of the diversity of fungal biocontrol systems, it will be necessary to determine safety on an individual species basis (1).

Safety procedures and evaluation criteria for Bacillus popilliae and B. thuringiensis are discussed by Heimpel (115). The guidelines for safety evaluation of microbial agents may be applicable to testing entomogenous bacteria.

Microsporida associated with vertebrates and crustaceans have been well documented (115). In rodents, unidentified Nosema spp. have been detected in tumors, in the brain, and in infections. Other microsporida are common parasites of fresh and salt water fish and crustaceans; these include shrimps and blue crabs. EPA guidelines are not sufficient for testing entomogenous protozoa. Current identification methods are inadequate and must be improved before microsporida can be seriously considered for testing. Promising approaches include serology and electrophoresis of protein digests.

SYSTEMS ANALYSIS AND MODELING

The application of systems analysis to biological control has received only limited study, although its value in describing, designing, testing, and managing this type of activity is recognized and documented (128, 213). As used here, systems analysis is a methodology that attempts to describe the behavior of complex biological systems. In practice, those systems are most often expressed as subcomponents in the form of conceptual flowcharts or as interconnected mathematical submodels. When applied to biological control, the method usually involves one or more of the following sequential activities: 1) The identification and quantitative description of the basic biological entities of the system (for example, biocontrol agent, host or prey, crop, alternate host or prey) in a stimulus/response form which includes the major biological and physical input variables which may influence their population dynamics; 2) the development of an overall descriptive systems model that couples these specific elements into a single coordinated system; 3) the incorporation of certain control elements or methodologies and economic factors into a management system; and 4) the development of an

implementation/action design for the operation of a practical biological control program. If a biological control program is largely unaffected by management or by manipulation, only activities 1 and 2 may be necessary to improve understanding; where intensive management is anticipated, all activities are required.

There are several potential benefits of using systems analysis methods to increase an understanding of how biological control operates. In the design of research, they help elucidate elements or factors to which the system is sensitive. This provides clues for determining the amount and degree of precision that should be sought in a given experiment. In the design of large-scale research projects, systems methods permit partitioning the system, provide a basis for allocation of labor, and keep the various facets of the research approach focused on the development of a coordinated system. Systems models may be used to test hypotheses concerning release strategies or population techniques before field trials are made. When used in connection with environmental data received from the field, they may function in a predictive management mode for decision making.

Several examples of systems models applicable to biological control are available (213); more are being developed and may be expected to become available soon (128). These range from general models of biological control processes, such as predator functional response models, to pest-specific population dynamics models concerned with specific biological control agents. As more attention is directed toward systems analysis and modeling, there will be an enormous increase in demand for the basic biological data that are necessary to describe submodels for the individual species involved. At this time we are only in the early stages of applying a new methodology that should greatly increase our understanding of the basic principles involved in the use of biological agents for pest control. A significant increase in the application of systems analysis to biological control activities is anticipated, and the combined benefits derived from model building, validation, simplification, integration, and economic and environmental impact analysis should lead to great improvement over the traditional methods of developing and implementing such control programs.

It is anticipated that systems analysis methodologies will contribute materially to the economic optimization of

biological control programs. In recent years, economists have been engaged in increasingly critical attempts to define the "economic threshold" concept in the context of biological control systems (86, 190, 202, 241). Conceptual mathematical models that combine equations relating pest and biotic agent population growth, pest damage, pest control costs, and other factors have been used to acquire a better understanding of the relationships between these several factors and the optimal timing and rate of control applications. The contributions of Feder and Regev (86) and Regev _et al._ (202) are of special significance because they deal with application of optimizing techniques to biological models that include predator-prey interactions.

Analytical biological models are difficult to build, and programming constraints limit models to the investigation of key relationships. Although improvements in this approach are forthcoming, it is unlikely that within the next several decades economic optimization criteria can be applied with certainty to the biological models that incorporate significant interrelationships between crop conditions and other important variables involving pests, their natural enemies, and agricultural production practices. Nevertheless, this approach should continue to provide better integrated insights into the management of complex agroecosystems, even though all relevant factors are not considered.

There is no sharp distinction between determining feasibility of using biological agents and implementing actual programs for pest control. The one tends to flow into the other, once a reasonable level of technical competence has been attained and questions concerning safety and economic benefits have been resolved satisfactorily. For example, the methods of system analysis may be expected to contribute materially to the determination of technical feasibility and cost/benefit ratios as well as providing guidelines for program implementation.

There remains, of course, determination of which of many pressing pest control problems deserves highest priority for implementation. Decision making of this kind considers not only the pest situation, the ecological disruptions, and the inherent nature of the pest species, but also the many socioeconomic factors that influence program priorities and the choice of control methods. It is important to remember that there are many ways of making adjustments

in a pest situation (184), and the objectives of this technical status report include not only the use of biocontrol agents _per se_, but also how those agents may be used in conjunction with other pest management strategies, either concurrently or sequentially and how such uses fit into the overall pattern of food and fiber production and use. In short, we are concerned with how biocontrol agents may best be used in resource management, the resource being the earth upon which we live.

VI. CONSIDERATIONS FOR IMPLEMENTING BIOLOGICAL CONTROL

The National Academy of Sciences reports (186) dealing with selected pest situations illustrate the complexities involved in developing and implementing pest control programs. Issues related to the use of biological agents in such programs have been touched upon in this report. The use of biological agents has many theoretical advantages: Relative permanence, lack of environmental contamination, energy conservation, and long-range economy. However, until arguments in favor of the method are more widely accepted and better opportunities for implementation of biological control programs made available, the use of biocontrol agents will be limited largely to those situations where efficacy of biological control is readily demonstrable. Because biological control methods tend to prevent rather than correct pest situations, it is difficult to compare the efficacy of the use of biological agents with that of other pest control tactics. Accordingly, pesticides will continue to be used, particularly in agriculture, forestry, and public health, even though alternative technologies may be known and are available. Effective use of biological agents will require more sources of different kinds of agents for use against specific pests and better dissemination of information regarding their use. This discussion of implementation deals with specific activities and supporting organizational structures needed for action programs, once feasibility determinations have been made. The discussion focuses on general considerations, delivery systems, organizational structures, and assessment of programs.

GENERAL CONSIDERATIONS

Different types of action programs are necessary to meet the broad spectrum of pest situations in which biological agents may be useful. The main factors to be considered in determining the action program needed are: The biological dimensions of the problem, the scope and temporal aspects of the contemplated operation, the integration and coordination of pest control tactics, and the legal and social aspects. The potential for program success is enhanced by appropriate prior attention to these interrelated factors.

Biological Characteristics

The biological characteristics of a pest situation are basic to all other considerations, and their relevance to decision-making cannot be overemphasized. The combined attributes of the pest, the biocontrol agents, and the affected resource will dictate the techniques that will be most suitable in a given pest situation. The fecundity of the pest, the duration of its life cycle, its mode of reproduction, and its potential for dispersal will profoundly influence the kinds of biocontrol agents that are appropriate and how they will be used. Microbial antagonists of plant pathogens are often present in the environment where a pest situation occurs, and the problem may be solved by cultural manipulations that invoke appropriate antagonistic reactions. A pest such as the cottonycushion scale can be kept under complete control by biological agents that are well adapted to its environment and capable of adjusting to its life cycle, so long as their activities are not disrupted by pesticides. Some aphids have the capacity to escape from predators such as *Chrysopa*, and increase their numbers enormously within a short span of time; thus, it may be necessary to mass produce the predator and release it in numbers at the sites where aphid populations are abundant or to introduce a more efficient natural enemy that could persist from season to season. Pests such as *Heliothis zea* are extremely mobile, but the viral pathogens that affect the larval stages do not move well in the environment; thus, it may become necessary to inoculate the pest population with the virus to initiate an epizootic situation. Biological considerations such as these determine whether biological control agent introductions, augmentative releases, management of endemic natural enemies, use of autocidal methods, modification of cultural practices, or a combination of tactics is desirable.

Scope and Temporal Aspects

Implementation of pest control programs using biocontrol agents is also influenced by spatial and temporal considerations. If the infested area is localized and the pest organism and biocontrol agents relatively immobile (for example, phytophagous and predatory mites on deciduous fruit trees; soil inhabiting plant pathogens and antagonists

endemic to a region), operational units of a few acres or an individual field may be reasonable. When pest situations embrace larger areas such as pulpwood forests or the corn belt, or when the pest has the ability and inclination for dispersal, operational units must be expanded accordingly, even to the level of national or international dimensions if necessary. Programs of regional scope or less are normally organized and managed on the basis of specific crops (for example, citrus, potatoes) or kinds of pests (Japanese beetles, *Armellaria* root rot) with which growers or communities are directly concerned. For example, the on-going program using biocontrol agents against the cereal leaf beetle in the North Central United States is multi-State in scope and will presumably become more extensive as the infested area expands. The international screwworm fly control program currently involves production and release of about 300 million sterile flies per week in the southwestern United States and Mexico during the spring and summer.

Time is an important element in the design and conduct of programs. For pest species that will produce economic damage, action against infestations, if amenable to biocontrol, is more likely to result in eradication or control if preventive measures are carried out before a reproductive cycle of the pest can occur. The comparative temporal dynamics of different crops, such as forests, perennial forage plants, annual field crops, or vegetable crops with short growth periods, as well as the biological characteristics of the associated pests and their biocontrol agents, will influence the frequency of monitoring activities and the duration of pest damage that can be tolerated. The number of generations of the pest and the biocontrol agents per season or per year or the asexual reproductive potential of each will affec the frequency of monitoring that is required to guide subsequent management activities.

Integration and Coordination

Biological control programs must be integrated with other resource management activities. Suppression tactics used against other pests may have unanticipated effects on biological agents used against the target pest; in addition, cultural practices in agriculture and forestry need to be considered. The ever-changing patterns of agricultural

production practices both complicate and enhance opportunities for success in coordination of biological, cultural, chemical, and other pest control methods. Stability and continuity are features of forest ecosystems that enhance the likelihood of long-term success in the use of biological agents for forest protection.

Success of a pest management program depends upon establishment of realistic economic or tolerance thresholds and necessitates careful sampling of pest populations. When biological control is a part of the management strategy, monitoring population trends of both pests and biocontrol agents is important, as is determination of the relative impact of the different management tactics employed. Care must be taken to assure that the different control strategies used are not incompatible. The most frequent conflicting interaction encountered in contemporary pest control programs is the adverse effects of insecticides on entomophagous biocontrol agents, usually by causing direct mortality. Other types of potential interactions include sublethal dosages of insecticides which may increase mortality from pathogens, use of soil fungicides or nematicides that adversely affect populations of beneficial antagonists, and use of insect growth regulators that adversely affect parasites attacking the same target pest. These and similar interactions must be taken into account.

The complexities of implementing a multifaceted pest control program in a crop management system are reflected in the compromises made in fruit tree insect pest management in the United States (124). Additional adjustments or compromises would presumably be required to resolve plant pathogen problems, and the economics of the entire production process need to be carefully analyzed. Pest management *per se* is but one of numerous identifiable and vital inputs necessary to crop management, as illustrated by citrus pest management (89).

Legal and Social Aspects

The enterprise of pest management is subject to a considerable range of legislation and regulation (186: vols. 1, 3). Directly and indirectly, regulations on development and registration affect the pest control methods that may be used and the extent and manner in which

agricultural products may be marketed. For the most part, legislative constraints focus on the use of pesticides. The extent to which insects or insect parts and microbial products are permissible or acceptable in marketed food is influenced by both legal regulations and consumer resistance. Biological control methods often result in less than complete elimination of pest populations, and thus the cosmetic standards for fruits and vegetables necessary to meet legal requirements, or thought to be needed to satisfy consumers, may not be attainable in some situations.

As discussed in connection with the Biological Agent Resource Centers, production of agents of known quality will be necessary. Present trends suggest that commercial production of biological control agents will involve meeting regulations on standards of quality and/or quantity per unit of activity. Persons or firms engaged in pest monitoring activities, pest control advisors, and pest control operators will likely be required to demonstrate proficiency in their occupations.

Efficient means of production and delivery of biocontrol agents are in the best interest of American agriculture. Government resources can be utilized to supply research and development information and to answer questions of efficacy and safety as needed. However, the private sector should become involved where feasible in the processing, production, and commercialization of biocontrol products that may range from live invertebrate organisms to packaged formulations of microbial materials. The private sector may also be involved in the development and operation of management systems in which biocontrol agents would be an integral part.

The marketing of some biocontrol agents or systems can be handled by private industry in side-by-side marketing with pesticides. Such an approach would allow for competitive profit-making development of some biocontrol agents. In comparison with chemical pesticides, however, a unique problem exists. Currently, biocontrol agents are not covered by patent laws. It is true that process patents can be obtained for manufacturing techniques or product formulations, but such patents provide limited protection.

To encourage commercial development of biocontrol agents, USDA should consider: (1) Making available efficacy and

safety data in a timely and orderly manner to allow industry to easily evaluate the product; and (2) supporting legislation to allow for a no-invention patent and permitting the licensee exclusivity during development and initial marketing to allow for a reasonable return on investment.

DELIVERY SYSTEMS

Delivery systems are essential for efficient and timely transfer of biological control agents and information regarding their use. The following elements are included: Biocontrol agent production facilities, distribution channels, including release or application techniques, and data collection, interpretation, and dissemination.

Biocontrol Agent Resource Centers

The need for importation mechanisms, quarantine facilities, and biological control agent resource centers, including production facilities, have been discussed previously. During large scale trials, most production problems will have been solved or anticipated. However, experience with several current programs has shown the importance of maintaining methods development research as a necessary facet of production activities (36).

The various kinds of institutions and organizations presently engaged in production of biocontrol agents, or likely to become involved, have been reviewed in a previous section of this report. The involvement of the U.S. Department of Agriculture in this activity has been reviewed (186: vol. 1). Although the patterns of production and supply that may eventually develop in the public or private sector are uncertain, it is clear that effective use of many biological control agents may depend upon the existence of reliable biocontrol agent resource centers and production facilities.

Distribution Channels

Presently utilized channels for the movement of biocontrol agents exist largely within the research community, except for material originating in a limited number of commercial

establishments and a few Government operated production facilities. A virtually untapped channel of distribution for these agents is through the State and Federal regulatory agencies which have developed considerable expertise in this area. Information regarding optimal techniques for handling, transport, storage, and release of specialized types of agents has not been collated and must be obtained as needed from research or regulatory agency scientists specializing in the particular field. Although the agencies concerned with biological control materials and methods have been reasonably successful in implementing several biological control projects, the expanded use of biocontrol agents for large-scale implementation programs will require a more highly organized and coordinated system.

Within Government agencies concerned with pest control programs, units having responsibility for distribution of biocontrol agents and information regarding methods of use should be clearly identified. The Animal and Plant Health Inspection Service of USDA has a network of employees across the country involved in such programs at the present time. The Extension Service and the Forest Service, through county agents, extension foresters, and State foresters in the States are appropriate channels for transmitting information to users once the necessary information comes available. Information similar to that provided in connection with production, distribution, and release of *Chrysopa carnea* (137, 183) is needed.

Data Collection, Interpretation, and Dissemination

The need to acquire reliable information about pest population levels, age structure, natural enemy populations, and related data concerning the state of the crop or resource is generally recognized. Such data are essential to the integration of multiple pest control tactics, establishment of realistic economic or tolerance thresholds, and effective decision making. For example, field data may be developed from research investigations or may be collected by growers, pest management specialists, or scouts employed for the purpose; climatic data are available from environmental monitoring networks. Decision making on the use of biocontrol agents will depend upon the objectives of the organizational units involved in that particular program.

Because of the many variables involved in agricultural and forest pest management programs, systems analysis techniques are being developed as an aid to decision making. The basic elements of such a management system are: (1) The biological system, that is, crops, pests, biocontrol agents, alternate hosts, and other associated organisms; (2) a biological monitoring component for sampling population densities and trends; (3) a climatic monitoring component; (4) computer simulation models of population dynamics of crop, target pest, and impact of biocontrol agents; (5) an extension specialist group that translates management system outputs into recommendations; and (6) action programs to be carried out by growers or public agencies. Data from action programs, together with climatic data, are fed back into the system to provide a basis for further decision making.

Before such a computerized management system can be developed, it is useful to develop simulation models for each of the major biological system components--crop plant, pests, and their natural enemies. These separate models can be simulated simultaneously by a computer to estimate the reaction of the biological system to exogenous factors such as weather or insecticide applications. Simulation models of insect pests usually depict the population in terms of age components; models of pathogens estimate population size and growth rate. A life system flow diagram for the corn earworm, *Heliothis zea*, is illustrated in a review of cotton pest control (186: vol. 3). MOTHZV-2 (108) is an example of a computer simulation of the population dynamics of two species of *Heliothis*. Bird *et al*. (19) have developed a model of population dynamics for nematodes on potato.

ORGANIZATIONAL STRUCTURES

The operational units concerned with the use of biocontrol agents may vary in size from individuals to governmental and international agencies. For optimal implementation of programs, there is need to establish coordinating units that provide inputs into planning and decision making and ensure that program objectives are carried out. These units may recommend situations in which the use of biocontrol agents appears feasible, assist in procurement of biological materials, and be involved in the exchange of information on implementation technology.

The several levels of organizational units are: Local, State and regional, national, and international. The extent to which participation of these various levels may be desirable or necessary depends upon the complexity of the pest situation, the kinds of agents used, and their general availability. Because each pest situation invariably has its own unique peculiarities, an organizational structure exactly congruent with the requirements of a specific situation seldom exists. Operational flexibility sufficient to permit adjustments to the needs of specific pest problems is necessary.

Local

The importance of actions by community groups, individual growers, ranchers and others in biological control programs should not be overlooked. These individuals are the key to initiating local environmental manipulations that may be desirable for plant pathogen and insect control or critical to the success of other types of programs. The use of phytophagous insects for the control of range and pasture weeds (for example, Klamath weed and tansy ragwort) in the western United States has been enormously expedited by redistribution of the agents from established population foci by individual ranchers. Individuals may also obtain and use agents that are available commercially or redistribute agents that occur naturally, as is often done with viral pathogens of lepidopterous pests such as the cabbage looper.

State and Regional

There are numerous county and State Government units, as well as Federal cooperating agencies, in existence that focus upon regional issues related to agriculture, forestry, and land use management. In addition, non-Governmental organizations such as grower or community cooperatives, pest management districts, or commodity oriented organizations have an interest in the impact of pest control practices. Greater efficiency would result if the efforts of individuals could be coordinated through such organizations, particularly if a collective approach to funding and the procurement and dissemination of materials could be arranged. Organizations appropriate for this type of program coordination include Farmer's

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Cooperatives (118), Mosquito Control and Abatement Districts (186: vol. 5), Pest Management Districts (72), and the Citrus Pest Management Program in Florida. Appropriate guidance may be obtained from the Land Grant University system, State and Federal pest control agencies, and Regional Plant Boards. Cooperation and communication among organizational units and with Experiment Station research and cooperative extension personnel is essential.

National

At the national level, implementation, technical assistance, and conduct of pest control programs are responsibilities of the USDA through its Animal and Plant Health Inspection Service (APHIS), Agricultural Research Service (ARS), Cooperative State Research Service (CSRS), Forest Service (FS), and Extension Service (ES). However, there is no single mechanism designed to provide coordination of the use of biocontrol agents for pest control. One approach to such an arrangement is the Working Group on Biological Control of Weeds of the Interdepartmental Weed Committees of the USDA and the U.S. Department of the Interior. That Working Group reviews programs that involve the introduction and distribution of biocontrol agents for weed control, primarily to determine if environmental hazards or conflicts of interest may arise if proposed action programs are implemented. In addition, ARS provides assistance to State and Federal organizations in procurement and distribution of biocontrol agents through the Working Group on Natural Enemies of Insects, Weeds, and other Pests (WGNE), which coordinates biocontrol activities among the several ARS laboratories. The USDA has also constituted an interagency Working Group on Biological Control Agents to study and make recommendations on all aspects of biocontrol.

A number of Federal agencies--Department of Defense, Department of the Interior, Department of Health, Education, and Welfare, Department of State, Environmental Protection Agency, and possibly others--have a variety of interests in biological control projects but no direct involvement in domestic program implementation. There is need for an action oriented organizational unit at the national level to provide leadership in the implementation of programs for biological control of pests. Such a unit should logically be located in the USDA, because it is the agency which has

the major role in research, development, and implementation of pest control programs. An appropriate recommendation to that effect is contained in the Summary and Recommendations in this report.

International

There are international organizations concerned with exchange of biological agents and implementation methodologies. Two of these are the International Organization for Biological Control (IOBC) and the Food and Agriculture Organization (FAO), although the latter is involved in implementation of programs to only a limited extent. In addition, the Commonwealth Institute of Biological Control provides procurement services for the biological control community on a fee basis through its headquarters in Trinidad, West Indies. Bilateral agreements for the exchange of information and biocontrol agents in agriculture and forestry exist between the United States and the Soviet Union, between the United States and Israel, and also informally between the United States and France and other countries. The United States and Canada have for years cooperated effectively, on an informal basis, in the introduction and use of biocontrol agents. The current screwworm and citrus blackfly control programs are joint efforts of the United States and Mexico. A recent account of organized programs to utilize natural enemies of pests in Canada, Mexico, and the United States is available (6). Any worldwide improvement in the exchange of information and materials will greatly enhance implementation possibilities.

ASSESSMENT OF PROGRAMS

Program assessment, in the broad sense, involves appraisal of the efficacy of the methods used to resolve pest situations, the impact of the methods on the environment, and the extent to which they are economically sound and socially acceptable. All these factors are obviously interrelated. The importance of program monitoring, as a means of determining the feasibility of controlling pests with biological agents, has been discussed in preceding sections of this report. Where possible, program monitoring should also be designed to provide data useful in making a realistic assessment of the economic

aspects of the program. Because the efficacy of biocontrol agents is greatly influenced by other resource management actions, a benefit/cost analysis of the effects of such agents, separate from those of other interlinked factors, becomes an exceedingly complex problem. The analysis is made even more difficult because many biological control methods are basically preventive rather than corrective in their relation to pest populations; thus, the problem becomes one of determining the economic benefits realized from something that does not develop, that is, a pest situation.

This section reviews the relevant economic issues bearing on the problem of benefit/cost analyses of using biocontrol agents and concludes with an agenda of topics that should be considered in the economic assessment of alternative strategies for pest control. The diverse economic aspects of present pest control technologies in an agro-ecosystem are discussed in detail in a recent report (186: vol. 2).

Biocontrol agents have been used deliberately against only about one-third of the likely target insect pests and against very few nematodes, plant pathogens, and weeds. Economic, as well as technical, factors account for this fact. The relative roles of various techniques of pest control are not fully understood, in part due to the lack of definitive information on the benefit/cost relationships of using alternative methods such as biocontrol agents. Problems of pesticidal resistance and such off-target effects as environmental disruptions and human health hazards must be included in the benefit/cost analysis for proper evaluation of any single method or combination of methods used for pest control. The difficulties of including these factors explicitly in analyses of benefits and costs contribute to the absence of clear incentives for using biological control agents and are the major economic reasons why such agents are not being used to their technically feasible limits.

Benefit/cost analysis of biocontrol agents consists of identifying: (1) What is being gained and what is being lost by the use of biocontrol agents; (2) who are the gainers and the losers; (3) what is the time span over which the benefits and costs accrue; and (4) what is the difference between benefits and costs after adjusting for the time element.

To the individual user, the short run benefit of pest control is the difference between the income from the sale of the final product and the cost of the pest control actions taken over the life span of the crop (113). If the cost of achieving the same level of control is higher for one method than for another, the difference between benefits and costs may in fact be unfavorable for a short period of time. But, the long run benefits of overcoming resistance problems and of reducing chemical applications, for example, could make the difference between benefits and costs favorable for users of biocontrol agents.

To society, the short run benefit of biocontrol agent use is the value of the food and fiber, and the cost is the expense of the biological method as a portion of production expenses. The advantages to society of using biocontrol techniques instead of other methods of pest control could include reduction of environmental and human health hazards. These are real and must be included in any societal accounting of production expenses. Because the actions of an individual seldom affect the food and fiber delivery system or the state of the environment and human health, there are few incentives for individuals to attempt to include both long term considerations and societal advantages in benefit/cost calculations. However, society as a whole is affected by these considerations. Thus, the economic problem of implementing biocontrol involves overcoming difficulties of measuring costs and benefits and inducing both individual and societal actions. In many cases this means that society must effect institutional changes such as establishing pest control districts to make it economically beneficial for producers to use biological methods. For example, in a California agroecosystem, lygus bug populations develop on but do not harm safflower; yet they do harm cotton, to which they migrate. Currently, safflower growers have no reason to control lygus bugs, and cotton growers are presumably disinclined to compensate safflower growers for the cost of taking care of the cotton growers' problem. Biological control would be ideal solution for this type of situation and could be implemented under the auspices of a pest control district.

A major attempt to evaluate the benefits and costs of reduced pesticide use strategies in the production of cotton, peanuts, and tobacco in the United States was undertaken in 1974 by the Council on Environmental Quality

and the Environmental Protection Agency (107, 255). These efforts document the probability of significant benefits from reduced pesticide usage by relying more upon natural enemies of pests of those crops in the major production areas. Because data for controls were inadequate, additional supportive evidence of benefits appear desirable (255).

A computer program for making benefit/cost comparisons of alternative pest management strategies has been prepared and used to make a preliminary evaluation of the benefits and costs of alternative boll weevil management strategies--eradication, optimal management, and present practices (64). On the basis of that evaluation, in some production areas a case can be made for including the use of biological agents as a part of the optimal management program. More valid conclusions from this program await the incorporation of crop supply-and-demand price elasticities to account for consumption and acreage changes due to price and profit variations resulting from pest losses and control costs. More elaborate benefit/cost frameworks which incorporate the very important social and environmental benefits from reduced pesticide use are being prepared by Federal agencies, for example, the Office of Pesticide Programs, EPA.

In the context of program evaluation, key research areas related to benefit/cost analysis can be identified. First, benefit/cost analysis can assist in identifying pest management problems that may be economically solved by the use of biological agents, either alone or in combination with other tactics. The reduction in control costs, off-target social and environmental costs, and the public costs of monitoring and enforcing must be sufficient to justify the research, regulatory, and implementation costs of using biocontrol agents. Methods are needed for determining which of the available biocontrol agents are likely to have potential economic, social, and environmental benefits greater than their probable costs. Hopefully, the assessment methodology will become sufficiently sophisticated to incorporate the various unique aspects of biological control methods.

Economists also need to be included in biological research design to insure that appropriate types of data are generated as early as possible for subsequent economic assessment. Similarly, methods should be developed to monitor the future economic implications of biological

control research in progress. Greater economic sophistication in problem area identification, research development, and monitoring should result in more success per dollar invested in biological control research and implementation and thereby increase the net gains of further investment in the biological approach.

Second, certain problems associated with benefit/cost analysis of using biological agents for pest control deserve special attention:

1) Fewer off-target social and environmental costs are associated with biological control as compared to certain chemical control methods. These advantages need to be evaluated in terms that can be incorporated into benefit/cost analysis. In some instances, economic research will produce methods for deriving adequate dollar estimates; in others, methods for determining upper and lower limits of impact will result.

2) At present, it is difficult to determine the true costs of biological control, whereas costs of chemical control are more easily determined. For example, in assessing the benefits and costs of pest scouting programs, it is difficult to determine the extent to which some participating extension personnel would have provided the same or very similar services to growers had there been no publicly supported pest scouting program. A related problem in evaluation is related to the fact that many biological agents cannot be patented, with the result that there is limited incentive for private producers to make such agents available in the needed quantity and variety.

3) Because knowledge cannot be owned and contained (190), the benefits of its use are difficult to quantify. For example, some growers participating in pest scouting programs use the knowledge from that program in managing fields that are not in the program. An assessment of only those fields in the program would understate the benefits; if fields in the control group included fields in which "leaked" knowledge was applied, the relative benefits of the pest scouting program would be further understated.

4) Effective pest management and other farm management practices such as fertilization, irrigation, pruning, etc., are interactive. For example, tillage practices profoundly affect pest situations (24, 101). Adequate methods are needed to evaluate the benefits and costs of major interactions. For example, it has been difficult to determine whether the larger yields of cotton by growers in California's

San Joaquin Valley who utilize independent pest management consultants are attributable to the differences in pest management strategies or to differences in other management practices. The dollar value of the larger yield is several times greater than the savings in pest management costs, so the problem is not simple.

5) Growers are interested in the stability of relatively high profits. Some biological controls may be more risky due to their greater dependence on environmental conditions. On the other hand, all but the most selective chemical controls have greater risks of secondary resurgence and reemergence than do biocontrol agents. Methods for evaluating and incorporating the significance of the various types of risks to on-site decision-makers need to be developed for inclusion in benefit/cost analyses. Also needed to be incorporated into the benefit/cost analysis is the difference in risk of starting with biological approaches and generally having the option of alternative approaches subsequent to biological control failure, as compared to starting with chemical approaches and generally _not_ having the option of switching to biological controls due to incompatibilities and time.

6) The time parameters for biological control and chemical control are grossly different. For example, use of a biological control agent may entail high initial costs, including crop losses for a short period, until it becomes self-sustaining; chemical control may entail lower initial costs but require repeated applications. This results in the classic economic problem of how to compare costs in different time periods, that is, determining the social rate of interest. This issue is further clouded in the case of pest management due to the mixture between private and public costs and benefits and private and public implementation roles. Appropriate methodologies for encompassing this issue can be developed for application to pest control program evaluation.

From the foregoing and other discussions of benefits and costs of different methods of pest control (186: vols. 1, 2), it is evident that there is need for a concerted effort to improve the methods used for economic analysis throughout the pest control enterprise. Ideally, means should be developed for assessing both the short- and long-run

benefit/cost ratios of different tactics when used separately or in concert. A program of research by interdisciplinary project teams composed of economists and biologists knowledgeable in the broad field of pest control technology should be established.

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APPENDIX

STATUTORY AUTHORITY FOR U.S. DEPARTMENT OF AGRICULTURE TO UNDERTAKE RESEARCH, EDUCATION, OR REGULATORY ACTION ON BIOLOGICAL AGENTS FOR PEST CONTROL

The United States Department of Agriculture has statutory authority to perform research, fund research by others, conduct educational programs, develop and disseminate informative materials, take regulatory action, and implement and effectuate these and other related activities through cooperative agreements with the States, other agencies, and foreign governments, in the area of biological agents for control of pests.

The following statutes provide authority for such activities by the Department.

Federal Insecticide, Fungicide, and Rodenticide Act, as amended

7 U.S.C. §136t(b) (June 25, 1947, ch. 125, §22, as added Oct. 21, 1972, Public Law (D.L.) 92-516, §2, 86 Stat. 996)	"Cooperation."
7 U.S.C. §136u(b) and (c) (June 25, 1947, ch. 125, §23, as added Oct. 21, 1972, P.L. 92-516, §2, 86 Stat. 996)	"Contracts for training."

The Mexican Pink Bollworm Act

7 U.S.C. §145 (Oct. 6, 1917, ch. 79, §1, 40 Stat. 374)	"Mexican pink bollworm; establishment of zones free from cotton culture; cooperation with Mexican officials."

Organic Act of 1944, as amended, and the Act of April 3, 1937, as amended

7 U.S.C. §147a (Sept. 21, 1944, ch. 412, title I, §102, 58 Stat. 735; June 17, 1949, ch. 220, 63	"Control and eradication of pests and plant diseases; cooperation of States and

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Stat. 200; May 23, 1957, P.L. 85-36, title II, §201, 71 Stat. 35)	farmers' associations, definition of State; rules and regulations; appropriations."
7 U.S.C. §148 (Apr. 6, 1937, ch. 69, 50 Stat. 57; May 9, 1938, ch. 192, 52 Stat. 344; Aug. 13, 1954, ch. 731, 68 Stat. 717)	"Control of insect pests and plant diseases."
7 U.S.C. §148a (Apr. 6, 1937, ch. 69, §2, as added May 9, 1938, ch. 192, 52 Stat. 344).	"Same; general administration; personnel; field work, etc."

The Golden Nematode Act

7 U.S.C. §150 (June 15, 1948, ch. 471, §1, 62 Stat. 442)	"Governmental policy for protection of potatoes and tomatoes from golden nematode."
7 U.S.C. §150a (June 15, 1948, ch. 471, §2, 62 Stat. 443)	"Duty of Secretary of Agriculture."
7 U.S.C. §150b (June 15, 1948, ch. 471, §4, 62 Stat. 443)	"Inspections; quarantines; restrictions; crop destruction; compensation of growers."
7 U.S.C. §150c (June 15, 1948, ch. 471, §4, 62 Stat. 443)	"Expenditure of funds; discretion of Secretary."
7 U.S.C. §150f (June 15, 1948, ch. 471, §7, 62 Stat. 443)	"Expenses; employment of personnel; printing and binding; purchase of passenger-carrying vehicles."

The Federal Plant Pest Act

7 U.S.C. §150aa-jj (P.L. 85-36, title I, §102, 103, 104, 105, 106, 107, 108, 109, 111, May 23, 1957, 71 Stat. 31, 32)	"Mailing of Plant Pests"

The Plant Quarantine Act

7 U.S.C. §160 (Aug. 20, 1912, ch. 308, §7, 37 Stat. 317)	"Regulations by Secretary restricting importation from insect-infested locality; hearing and promulgation of regulations; when quarantine effective."
7 U.S.C. §161 (Aug. 20, 1912, ch. 308, §8, 37 Stat. 318; Mar. 4, 1917, ch. 179, 39 Stat. 1165; Apr. 13, 1926, ch. 135, 44 Stat. 250)	"Interstate quarantine; shipment or removals from quarantined localities forbidden; regulations by by Secretary for shipment, etc., from quarantined localities; notice and hearing; promulgation."
7 U.S.C. §162 (Aug. 20, 1912, ch. 308, §9, 37 Stat. 318)	"Rules and regulations."
7 U.S.C. §164a (Aug. 20, 1912, ch. 308, §10, as added May 1, 1928, ch. 462, 45 Stat. 468)	"Enforcement of quarantine against nursery stock and plant products; search and seizure."
7 U.S.C. §167 (Aug. 20, 1912, ch. 308, §15, as added May 31, 1920, ch. 217, 41 Stat. 726 and amended May 16, 1928, ch. 572, 45 Stat. 565; July 7, 1932, ch. 443, 47 Stat. 640; Mar. 26, 1934, ch. 89, 48 Stat. 640; Mar. 26, 1934, ch. 89, 48 Stat. 486; July 29, 1970, P.L. 91-358, title I, §155(a), 84 Stat. 570)	"Rules governing District of Columbia."

Smith-Lever Act as amended 1953, 1955, 1962, 1972

7 U.S.C. §341 (May 8, 1914, ch. 79, §1, 38 Stat. 372; June 26, 1953, ch. 157, §1, 67 Stat. 83)	"Cooperative extension work by colleges."

7 U.S.C. §342, (May 9, 1914, ch. 79, §2, 38 Stat. 373; June 26, 1953, ch. 157, §1 67 Stat. 84; Oct. 5, 1962, P.L. 87-749, §1(a), 76 Stat. 745)	"Cooperative agricultural extension work; cooperation with Secretary of Agriculture."
7 U.S.C. §343 (May 8, 1914, ch. 79, §3, 38 Stat. 373; June 26, 1953, ch. 157, §1, 67 Stat. 84; Oct. 5, 1962, P.L. 87-749, §1 (b)-(e), 76 Stat. 745; as amended June 23, 1972, P.L. 92-318, title V, §506(g), 86 Stat. 351)	"Appropriations: distribution; allotment and apportionment; Federal Extension Service."
7 U.S.C. §344, (May 8, 1914, ch. 79, §4, 38 Stat. 374; June 26, 1953, ch. 157, §1, 67 Stat. 85; Oct. 5, 1962, P.L. 87-749, §1(f), 76 Stat. 745)	"Ascertainment of entitlement; time and manner of payment; reports of receipts and disbursements."
7 U.S.C. §347a (May 8, 1914, ch. 79, §8, as added Aug. 11, 1955, ch. 798, §1(a), 69 Stat. 683, and amended Oct. 5, 1962, P.L. 87-749, §1(h), 76 Stat. 745)	"Disadvantaged agricultural areas"
7 U.S.C. §348 (May 8, 1914, ch. 79, §9, formerly 8, 38 Stat. 374, amended June 26, 1953, ch. 157, §1, 67 Stat. 85, renumbered Aug. 11, 1955, ch. 798, §1(b), 69 Stat. 684)	"Rules and regulations."
"Chap. 14 (Agricultural Experiment Stations)" Hatch Act of 1887, as amended, and law supplementary thereto, P.L. 84-353; Adams Act of 1906; Purnell Act of 1925; Bankhead-Jones Act of 1935; and the Agricultural Marketing Act of August 14, 1946.	

7 U.S.C. §361a (Mar. 2, 1887, ch. 314, §1, 24 Stat. 440; Aug. 11, 1955, ch. 790, §1, 69 Stat. 671, P.L. 93-471; Oct. 26, 1974, 88 Stat. 1423, as amended June 23, 1972, P.L. 92-318, title V, §506(k), 86 Stat. 351; Oct. 26, 1974, P.L. 93-471, title II, §208 (e), 88 Stat. 1429)	"Congressional declaration of purpose; definitions."
7 U.S.C. §361b (Mar. 2, 1887, ch. 314, §2, 24 Stat. 440; Aug. 11, 1955, ch. 790, §1, 69 Stat. 671)	"Congressional statement of policy; researches, investigations and experiments."
7 U.S.C. §361c (Mar. 2, 1887, ch. 314, §3, 24 Stat. 441; Aug. 11, 1955, ch. 790, §1, 69 Stat. 671.	"Appropriations and allotments of grants."
7 U.S.C. §361d (Mar. 2, 1887, ch. 314, §4, 24 Stat. 441; Aug. 11, 1955, ch. 790, §1, 69 Stat. 672)	"Use of funds."
7 U.S.C. §361g (Mar. 2, 1887, ch. 314, §7, 24 Stat. 441; Aug. 11, 1955, ch. 790, §1, 69 Stat. 673; June 29, 1960, P.L. 85-533, §1(22), 74 Stat. 249)	"Secretary of Agriculture; powers and duties; rules and regulations; determination of amount of entitlement; deduction of unexpended balances."
7 U.S.C. §427 (June 29, 1935, ch. 338, §1, 49 Stat. 436; Aug. 14, 1946, ch. 966, title I, §101, 60 Stat. 1082)	"Agricultural research; declaration of policy; duties of Secretary of Agriculture; use of existing facilities."
7 U.S.C. §427i (June 29, 1935, ch. 338, §10, as added Aug. 14, 1946, ch. 966, title I, §101, 60 Stat. 1085, and amended July 28, 1954, ch. 591, 68 Stat. 574)	"Agricultural research; additional appropriations; administrative expenses; availability of special research fund."

Agriculture Act of 1970, as amended by Agricultural and Consumer Protection Act of 1973

7 U.S.C. §428a (Aug. 3, 1956, ch. 950, §11, 70 Stat. 1034)	"Acquisition of land; options."
7 U.S.C. §428b P.L. 91-524, title VIII, §810, as added P.L. 93-86, §1(27)(B), Aug. 10, 1973, 87 Stat. 238)	"Wheat andd feed grains research; regional and national research programs; utilization of services of Federal, State and private agencies; authorization of appropriations."
7 U.S.C. §428 (P.L. 91-524, title VIII, §810, as added P.L. 93-86, §1(27)(B), Aug. 10, 1973, 87 Stat. 238)	"Wheat and feed grains research; regional and national research programs; utilization of services of Federal, State and private agencies; authorization of appropriations."

Talmadge-Aiken Act

7 U.S.C. §450 (P.L. 87-718, Sept. 28, 1962, 76 Stat. 663)	"Cooperation with State agencies in administration and enforcement of laws relating to marketing of agricultural products and control or eradication of plant and animal diseases and pests; coordination of administration of Federal and State laws."
7 U.S.C. §450a (P.L. 88-250, title I, §101, Dec. 30, 1963, 77 Stat. 820)	"Cooperative research projects; agreements with and receipt of funds from State and other agencies."
7 U.S.C. §450b (July 24, 1919, ch. 26, 41 Stat. 270)	"Cooperation with State and other agencies; expenditures."
7 U.S.C. §450i (P.L. 89-106, §2, Aug. 4, 1965, 79 Stat. 431)	"Research grants; duration; records; audit."

7 U.S.C. §1444a(c)	"Cotton research program; reduction of upland cotton production costs; authorization of appropriations; reports to Congressional committees."
7 U.S.C. §1444a(d) (Oct. 31, 1949, ch. 792, title I, §104, as added Aug. 28, 1958, P.L. 85-835, title II, §201, 72 Stat. 993, and amended Apr. 11, 1964, P.L. 88-297, title I, §103(a), 78 Stat. 174; Nov. 30, 1970, P.L. 91-524, title VI, §611, as added Aug. 10, 1973, P.L. 93-86, §1(24), 87 Stat. 235).	"Cotton insect eradication; Commodity Credit Corporation execution of program; utilization of technical and related services of Federal, State, and private agencies and cotton organizations; participation and cooperation of beneficiaries of any program."

Subchapter III - Land Conservation and Land Utilization

7 U.S.C. §1010a (P.L. 92-419, title III, §302, Aug. 30, 1972, 86 Stat. 670)	"Soil, water and related resource data; report."
7 U.S.C. §1011 (As amended Aug. 30, 1972, P.L. 92-419, title III, §301, 86 Stat. 669)	"Powers of Secretary of Agriculture."

The Agricultural Marketing Act of 1946, as amended

7 U.S.C. 1621 (Aug. 14, 1946, ch. 966, title II, §202, 60 Stat. 1087)	"Congressional declaration of purpose; use of existing facilities; cooperation with States."
7 U.S.C. 1622 (Aug. 14, 1946, ch. 966, title II, §203, 60 Stat. 1087; Aug. 9, 1955, ch. 632, §1, 69 Stat. 553)	"Duties of Secretary relating to agricultural products."
7 U.S.C. §1623 (Aug. 14, 1946, ch. 966, title II, §204, 60 Stat 1089)	"Appropriations; allotments to States."

7 U.S.C. §1624 (Aug. 14, 1946, ch. 966, title II, §205, 60 Stat. 1090; Aug. 30, 1954, ch. 1076, §1(7), 68 Stat. 966)	"Cooperation with government and State agencies, private research organizations, etc.; rules and regulations."
7 U.S.C. §1625 (Aug. 14, 1946, ch. 966, title II, §206, 60 Stat. 1090)	"Transfer and consolidation of functions, powers, bureaus, etc."
7 U.S.C. §1626 (Aug. 14, 1946, ch. 966, title II, §207, 60 Stat. 1091)	"Definitions."
7 U.S.C. §1627 (Aug. 14, 1946, ch. 966, title II, §208, 60 Stat. 1091)	"Appointment of personnel; compensation; employment of specialists."

Agricultural Trade Development and Assistance Act of 1954

7 U.S.C. §1691 (July 10, 1954, ch. 469, 68 Stat. 454; Nov. 11, 1966, P.L. 89-808, 80 Stat. 1526, as amended Dec. 20, 1975, P.L. 94-161, title II, §201, 89 Stat. 850)	"Declaration of policy."
7 U.S.C. §1704 (As amended Dec. 20, 1975, P.L. 94-161, title II, §204, 89 Stat. 852)	"Purposes for which foreign currencies may be used."

Chapter 43 - Agricultural Attaches

7 U.S.C. §1762 (Aug. 28, 1954, ch. 1041, title VI, §607, 68 Stat. 908; June 28, 1955, ch. 189, §12(c) (13), 69 Stat. 182; Aug. 4, 1965, P.L. 89-106, §4, 79 Stat. 431)	"Personnel."

Chapter 55 - Department of Agriculture

7 U.S.C. §2201 (As amended P.L. 92-419, title VI, §603(a), Aug. 30, 1972, 86 Stat. 675)	"Establishment of Department."

7 U.S.C. §2204 (As amended P.L. 92-419, title VI, §603(b), Aug. 30, 1972, 86 Stat. 675)	"General duties of Secretary; advisory functions; National rural development program; report to Congress."
7 U.S.C. §2250a (P.L. 89-106, §1, Aug. 4, 1965, 79 Stat. 431)	"Erection of buildings and other structures on non-Federal lands; duration of use of such lands; removal of structures after termination of use; availability of funds for expenses of acquiring long-term leases or other agreements."
7 U.S.C. §2263 (P.L. 89-106, §8, Aug. 4, 1965, 79 Stat. 432)	"Transfer of funds."

Chapter 59 - Rural Fire Protection, Development and Small Farm Research and Education

7 U.S.C. §2661 (P.L. 92-419, title V, §501, Aug. 30, 1972, 86 Stat. 671)	"Statement of purposes."
7 U.S.C. §2662 (P.L. 92-419, title V, §502, Aug. 30, 1972, 86 Stat. 671)	"Programs authorization; cooperation and coordination with colleges and universities.
7 U.S.C. §2663 (P.L. 92-419, title V, §503, Aug. 30, 1972, 86 Stat. 672)	"Program moneys."
7 U.S.C. §2664 (P.L. 92-419, title V, §504, Aug. 30, 1972, 86 Stat. 673)	"Cooperating colleges and universities."
7 U.S.C. §2665 (P.L. 92-419, title V, §505, Aug. 30, 1972, 86 Stat. 673)	"Agreements and plans."
7 U.S.C. §2667 (P.L. 92-419, title V, §507, Aug. 30, 1972, 86 Stat. 674)	"Definitions."

7 U.S.C. §2668 (P.L. 92-419 title V, §508, Aug. 30, 1972, 86 Stat. 674)	"Regulations."

Clarke-McNary Act

16 U.S.C. §471 (Mar. 3, 1891, ch. 561, §24, 26 Stat. 1103; Mar. 4, 1907, ch. 2907, 34 Stat. 1271; June 25, 1910, ch. 421, §2, 36 Stat. 847; Aug. 24, 1912, ch. 369, 37 Stat. 497; June 7, 1924, ch. 348, §9, 43 Stat. 655)	"National forests; establishment; uses; cooperation by Secretary of Agriculture with State Officials."
16 U.S.C. §505 (June 7, 1924, ch. 348, §9, 43 Stat. 655)	"Uses of national forests established on land reserved for purposes of national defense; maintenance available."

Chapter 3 - Forests; Forest Service; Reforestation; Management

16 U.S.C. §565a-1 (P.L. 94-148, §1, Dec. 12, 1975, 89 Stat. 804)	"Cooperative agreements between Secretary of Agriculture and public or private agencies, organizations, institutions, and persons covering Forest Service programs; authority; funding."

Knutson-Vandenburg Act

16 U.S.C. §576 (June 9, 1930, ch. 416, §1, 46 Stat. 527)	"Reforestation; establishment of forest tree nurseries; tree planting; seed sowing and forest improvement work."

McSweeney-McNary Act of 1928, as amended

16 U.S.C. §581 (May 22, 1928, ch. 678, §1, 45 Stat. 699; Apr. 24, 1950, ch. 97, §17(a), 64 Stat. 87)	"Authorization of investigations, experiments, and tests; cooperation with State and other agencies; appropriations and contributions; buildings; existing laws."
16 U.S.C. §581a (May 22, 1928, ch. 678, §2, 45 Stat. 700; June 15, 1936, ch. 553, 49 Stat. 1515)	"Forest experiment stations; establishment; appropriations."
16 U.S.C. §581b (May 22, 1928, ch. 678, §3, 45 Stat. 701)	"Diseases of forest trees and products; appropriation for investigations."
16 U.S.C. §581c (May 22, 1928, ch. 678, §4, 45 Stat. 701)	"Forest insects; appropriation for investigations."
16 U.S.C. §581d (May 22, 1928, ch. 678, §5, 45 Stat. 701)	"Life histories and habits of forest animals, birds, and wildlife; appropriation for experiments and investigations."

Forest and Rangeland Resources Planning Act of 1974

16 U.S.C. §581h (As amended Aug. 17, 1974, P.L. 93-378, §2(b), 88 Stat. 476)	"Present and prospective requirements for renewable resources; comprehensive survey and analysis by Secretary of Agriculture; implementation and cooperation by Secretary; authorization of appropriations."

Research Programs

16 U.S.C. §582a (P.L. 87-788, §1, Oct. 10, 1962, 76 Stat. 806)	"Congressional findings."

16 U.S.C. §582a-1 (P.L. 87-788, §2, Oct. 10, 1962, 76 Stat. 806)	"Cooperation by Secretary of Agriculture with States; assistance; plans, eligible institutions and amount."
16 U.S.C. §582a-5 (P.L. 87-788, §6, Oct. 10, 1962, 76 Stat. 807)	"Rules and regulations; cooperative State forestry research unit; advisory committee; Federal and State agency representation; annual advice to Secretary of Agriculture and national advisory board."
16 U.S.C. §582a6 (P.L. 87-788, §7, Oct. 10, 1962, 76 Stat. 807)	"Scope of forestry research."

Chapter 3B - Soil Conservation

16 U.S.C. §590g (As amended Aug. 30, 1972, P.L. 92-419, title VI, §606(1), 86 Stat. 676)	"Additional policies and purposes"
16 U.S.C. §590h (As amended Aug. 30, 1972, P.L. 92-419, title VI, §605, 606(2)-(5), 86 Stat. 676, 677)	"Payments and grants of aid."
16 U.S.C. §590o (As amended Aug. 30, 1972, P.L. 92-419, title VI, §606(6), 86 Stat. 677)	"Appropriations for purposes of sections 590g and 590h; allocation of funds among commodities."

Forest Pest Control Act

16 U.S.C. §594-1 (June 25, 1947, ch. 141, §1, 61 Stat. 177)	"Protection of all forest lands from insects and diseases; policy of Government."
16 U.S.C. §594-2 (June 25, 1947, ch. 141, §2, 61 Stat. 177)	"Same; conduct of surveys; consent to operations."
16 U.S.C. §594-3 (June 25, 1947, ch. 141, §3, 61 Stat. 177)	"Same; allocation of funds."

16 U.S.C. §594-4 (June 25, 1947, ch. 141, §4, 61 Stat. 177)	"Same; contributions to work."
16 U.S.C. §594-5 (As amended June 20, 1975, P.L. 94-40, 89 Stat. 224)	"Same; appropriations; availability for expenses; procurement of materials and equipment."

White Pine Blister Rust Control Act

16 U.S.C. §594a (Apr. 26, 1940, ch. 159, 54 Stat. 168)	"White-pine blister rust control; contributions by local authorities; Indian lands."

Fish and Wildlife Coordination Act

16 U.S.C. §611 (Mar. 10, 1934, ch. 55, §1, 48 Stat. 401; 1939 Reorg. Plan No. II, §4(e), (f), eff. July 1, 1939, 4 F.R. 2731, 53 Stat. 1433; Aug. 14, 1946, ch. 965, 60 Stat. 1080; Aug. 12, 1958, P.L. 85-624, §2, 72 Stat. 563)	"Declaration of purpose; cooperation of agencies; surveys and investigations; donations."

Chapter 18 - Watershed Protection and Flood Prevention

16 U.S.C. §1001 (As amended Aug. 30, 1972, P.L. 92-419, title II, §201(a) 86 Stat. 667)	"Declaration of policy."
16 U.S.C. §1002 (As amended Aug. 30, 1972, P.L. 92-419, title II, §201(b), 86 Stat. 667)	"Definitions."
16 U.S.C. §1003 (As amended Aug. 30, 1972, P.L. 92-419, title II, §201(c), 86 Stat. 667)	"Assistance to local organizations."
16 U.S.C. §1004 (As amended Aug. 30, 1972, P.L. 92-419, title II, §201(d)-(f), 86 Stat. 668)	"Conditions for Federal assistance."

16 U.S.C. §1005 (As amended Aug. 30, 1972, P.L. 92-419, title II, §201(g), 86 Stat. 669)	"Works of improvement."

Endangered Species Act of 1973

16 U.S.C. §1536 (P.L. 93-205, §7, Dec. 28, 1973, 87 Stat. 892)	"Interagency cooperation."

Chapter 16A - Grants for Support of Scientific Research

42 U.S.C. §1891 (P.L. 85-934, §1, Sept. 6, 1958, 72 Stat. 1793)	"Authorization to make grants."
42 U.S.C. §1892 (P.L. 85-934, §2, Sept. 1958, 72 Stat. 1793)	"Same; title to equipment."

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[illegible] U.S.C. §[illegible] (as amended [illegible], 1971, Pub. L. [illegible], [illegible], 85 Stat. [illegible])	"Works of improvement."

[illegible] Act of 1977

15 U.S.C. §1538 (P.L. 93-[illegible], [illegible], Dec. 28, 1973, 87 Stat. [illegible])	"[illegible] cooperation."

Chapter 16A - Grants for Support of Scientific Research

42 U.S.C. §1891 (P.L. 85-934, 85, Sept. 6, 1958, 72 Stat. 1793)	"Authorization to make grants."
42 U.S.C. §1892 (P.L. 85-934, 85, Sept. 1958, 72 Stat. 1793)	"Grant title to equipment."

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